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TEXT-BOOK OF PALAEONTOLOGY

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TEXT-BOOK

OF

PALAEONTOLOGY

BY

KARL A. VON ZITTEL

LATE PROFESSOR OF GEOLOGY AND PALAEONTOLOGY IN THE UNIVERSITY OF MUNICH

VOL. III. MAMMALIA

REVISED BY

MAX SCHLOSSER, PH.D.

CURATOR OF THE GEOLOGICAL MUSEUM AT MUNICH

TRANSLATED UNDER THE DIRECTION OF

CHARLES R. EASTMAN, PH.D.

BY

LUCY P. BUSH AND MARGUERITE L. ENGLER

TRANSLATION REVISED, WITH ADDITIONS,

BY

SIR ARTHUR SMITH WOODWARD, F.R.S.

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EDITORS' PREFACE

More than twenty years have elapsed since the original edition of Professor von Zittel's *Grundzüge der Paläontologie* was published. During the interval no department of the science has made greater advances than that which deals with fossil vertebrates, especially Mammals. The chapter treating of the Mammalia in the *Grundzüge* was twice revised by the author during his life-time, and the text was further enlarged by his colleague Dr. Max Schlosser, custodian of the geological and palaeontological collections in the Alte Akademie at Munich.

The present version is a literal rendering into English of Dr. Schlosser's revised account of the Mammalia, and the manuscript of the latter half of the translation has been critically examined by him. Dr. Schlosser has also supplied several new figures which do not appear in the earlier German editions.

The section comprising the *Eplacentalia* and the *Placentalia* onward as far as the *Perissodactyla*, also the *Notoungulata* and a portion of the *Subungulata*, has been translated by Miss Marguerite L. Engler, of New York, and the remaining part, comprising about a hundred pages of text in the original, by Miss Lucy P. Bush, formerly assistant to Professor O. C. Marsh at New Haven. The introductory pages were put in their present form by Professor F. B. Loomis, Amherst College. The task of the Editor has been limited to a supervision of the work and preparing the completed manuscript for printing.

CHARLES R. EASTMAN.

American Museum of Natural History,
New York, *Feb.* 1, 1916.

The revision of this volume was unfortunately left unfinished by the death of Dr. Eastman in 1918, and I have endeavoured to complete his work. With the help of Baron Francis Nopcsa, I have compared the whole of the English translation with the original German text, and made such emendations as seemed necessary. I have also added the more important recent discoveries, and have particularly extended the bibliographies with some references to the later literature.

A. SMITH WOODWARD.

Hill Place, Haywards Heath,
Sussex, *April* 30, 1925.

PUBLISHERS' NOTE

DR. EASTMAN'S version of the third German edition was nearly all in type, though unrevised, at the time of his death. This therefore forms the framework of the present English edition, which, however, has been brought up to date in all important particulars by Sir Arthur Smith Woodward.

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MAMMALIA. (Mammals.)[1]

Warm-blooded terrestrial or aquatic animals with external covering consisting of hair, usually forming a thick fur; never with scaly or feathered covering; a four-chambered heart present; skull with two occipital condyles; coracoid (except in Monotremes) vestigial and fused with the scapula. Lower jaw consisting of a single piece, articulating with the squamosal. Appendages developed as limbs, more rarely as fins, or the anterior pair as hands.

Among vertebrates the Mammalia constitute the most highly organised class. Their functions are more diversified and specialised, their nervous system

[1] Literature: *Ameghino, F.*, Contribución á conocimiento de los mamíferos de la Republica Argentina. Buenos Aires, 1889.—Énumération synoptique des espèces de mammifères fossiles des formations éocènes de Patagonie. Buenos Aires, 1894.—Première contribution à la connaissance de la faune des couches à Pyrotherium. Boletin del Inst. Geogr. Argentino, vol. xv., 1895.—Mammifères crétacés de l'Argentine.—*Ibid.* vol. xviii., 1897.—Ongulés nouveaux des terrains crétacés de Patagonie. Boletin Acad. Nac. de Cordoba, 1901.—Mammifères nouveaux des terrains crétacés. *Ibid.* 1902.—*Andrews, C. W.*, Descriptive catalogue of the Tertiary vertebrata of the Fayum, Egypt. London, 1906.—*Blainville, H. D.*, Ostéographie, ou déscription iconographique des mammifères. 4 vols., Paris, 1839–64.—*Cope, E. D.*, Vertebrata of the Tertiary formations of the West. Rept. U.S. Geol. Survey of Territories, vol. iii., 1884.—Synopsis of the Fauna of the Puerco Series. Trans. Amer. Phil. Soc., 1889, vol. xvi.—*Cuvier, G.*, Recherches sur les ossements fossiles. 1st ed., Paris, 1812. 4th ed., 1834–36.—*Depéret, C.*, Archives du Muséum d'Hist. Nat. Lyon, vol. iv., 1886; vol. v., 1892.—Les animaux pliocènes de Roussillon. Mém. Soc. Géol. de France, 1890.—Les vertébrés oligocènes de Pyrimont (Savoie). Mém. Soc. Paléont. Suisse, vol. xxix., 1902.—*Falconer, H.*, and *Cautley, P. T.*, Fauna antiqua sivalensis. London, 1846–49.—*Filhol, H.*, Ann. Sci. Géol., vol. iii., 1872; v., 1874; vii., 1876; viii., 1877; x., 1879; xiv., 1883; xvii., 1885; xxi., 1891.—*Flower, W. H.*, Introduction to the osteology of the mammalia. 3d ed., London, 1885.—*Gaudry, Albert*, Animaux fossiles et géologie de l'Attique. Paris, 1862–67.—Animaux fossiles du Mont Léberon (Vaucluse). Paris, 1873.—Les enchaînements du monde animal dans les temps géologiques; Mammifères tertiaires. Paris, 1878.—Fossiles de Patagonie. Annales de Paléont., vols. i. and ii., 1906.—*Gervais, P.*, Zoologie et paléontol. françaises. Paris, 1859.—*Giebel, G.*, and *Leche, W.*, Die Säugetiere, in Bronn's Classen und Ordnungen des Tierreichs. Bd. vi., 5th Abth., 1874–1906.—*Gregory, W. K.*, The orders of mammals. Bull. Amer. Mus. Nat. Hist., 1910.—*Hofmann, A.*, Die Fauna von Göriach. Abh. k. k. Geol. Reichsanst. Wien, 1893.—*Leidy, Joseph*, The extinct mammalian fauna of Dakota and Nebraska. Journ. Acad. Nat. Sci. Philad., vii., 1869.—*Lemoine, V.*, Mammifères fossiles de Reims. Bull. Soc. Géol. France, 1883–85, 1889.—*Lydekker, R.*, Catalogue of the fossil mammalia in the British Museum, parts i.-v. London; 1885–87.—Indian Tertiary and Pre-tertiary vertebrata. Palaeontol. Indica. Mem. Geol. Surv. India, ser. x., vols. i.-iv., 1875–1886.—Palaeontologia Argentina, Ann. Museo de la Plata, vol. ii., 1894.—*Matthew, W. D.*, Numerous papers in Bull. Amer. Mus. Nat. Hist. New York, 1897–1909.—Fossil Mammals of Northeastern Colorado. Mem. Amer. Mus., 1901.—*Osborn, H. F.*, Numerous articles and memoirs published by Amer. Mus. New York, 1892–1924.—The Age of Mammals. New York, 1911. —*Osborn* and *Scott*, Trans. Amer. Phil. Soc. vol. xvi., 1889.—*Roger, O.*, Verzeichnis der fossilen Säugetiere. Ber. Nat. Ver. Augsburg, 1896.—*Rütimeyer, L.*, Eocäne Säugetiere aus dem Schweizer. Jura. Denkschr. Schweiz. Ges. Gesammt. Naturwiss. xix., 1862.—Abh. Schweiz. Palaont. Ges. xviii., 1891.—*Schlosser, M.*, Die Säugetiere aus den süddeutschen Bohnerzen. Paläont. Abh., 1902.—Die fossilen

and sense-organs are better developed, and their dentition and limbs are more extensively differentiated than in any other class of animals. Only reptiles and fishes are comparable with mammals in the multiplicity of their adaptations. With the single exception of the monotremes the offspring is born alive. The embryos are provided with amnion and allantois. For a longer or shorter period the young are nourished on milk, secreted from the mother's mammary glands.

The vertebral column of mammals is divisible into five regions: cervical, dorsal, lumbar, sacral and caudal (the sacral region being undifferentiated only in the Cetacea and Sirenia). The vertebral centra do not present articular faces to each other as in reptiles and birds, but their plane surfaces are separated by discs or pads of fibro-cartilage; only the cervicals of certain ungulates depart from this rule, being united by opisthocoelous articulations. Each vertebra consists of a middle part, or centrum, to which are applied two thin discs of bone, the epiphyses, one at either end. On the centrum rest the two neural arches which early unite with each other and the centrum, all five elements fusing in the adult into a single bone, the vertebra.

The neck usually consists of seven vertebrae, the length depending on the elongation of the individual components. The transverse processes are perforated at their bases, forming a canal for the anterior vertebral artery.

The first cervical, the atlas (Fig. 1), is distinguished by the lack of a centrum and spinous processes, and by the extensive development of the transverse processes, the bases of which at the front end are excavated into two deep articular cups which receive the condyles on the back of the skull. Posteriorly the atlas has a broad

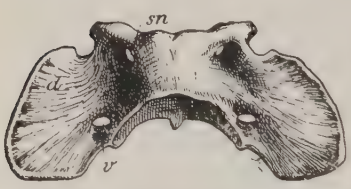

FIG. 1.

First cervical vertebra (atlas) of the dog (dorsal view). *d*, Expanded transverse process; *v*, arterial canal; *sn*, nerve canal.

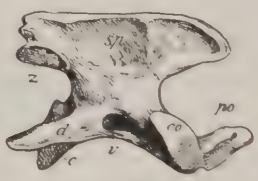

FIG. 2.

Second cervical vertebra (axis) of the dog (lateral aspect). *sp*, Neural spine; *c*, centrum; *d*, diapophysis; *z*, post-zygapophysis; *v*, arterial canal; *po*, odontoid process; *co*, articular surface for the atlas.

FIG. 3.

Sixth cervical vertebra of the dog (posterior aspect). *c*, Centrum; *sp*, neural spine; *n*, upper arch; *d*, diapophysis; *p*, parapophysis with inferiorly elongated lamella; *v*, arterial canal; *m*, neural canal; *z*, anterior; *z'*, posterior zygapophysis.

vertical articular facet for the second cervical or epistropheus (axis). This latter (Fig. 2) is distinguished by having in front a strong, conical, semi-cylindrical, or spout-shaped odontoid process; which, as shown by its development, is the centrum of the atlas.

The dorsal vertebrae (Fig. 4, *A*) are distinguished by having short centra, long spinous processes, and the facets for the heads of the ribs: one for the tuberculum, on the transverse process, and one for the capitulum, on the anterior

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Säugetiere Chinas. Abh. k. bayer. Akad. d. Wiss. II. Cl., vol. xxii., 1903.—*Scott, W. B.*, A History of Land Mammals in the Western Hemisphere. New York, 1913.—*Scott, W. B.*, and *Sinclair, W. J.*, Mammalia of the Santa Cruz Beds. Rept. Princeton University Expedition to Patagonia, 1903–1909.—*Weber, M.*, Die Säugetiere. Jena, 1904.—*Wortman, J. L.*, Articles in Bull. Amer. Mus. Nat. Hist. New York, 1892-99, and Amer. Journ. Sci., 1901 1902.

part of the centrum. The articular surface of the anterior zygapophysis looks upward, while that of the postzygapophysis looks downward. The first vertebra, which supports a rib united to the sternum, is commonly called the first dorsal. As a rule there are thirteen dorsals, less frequently from ten to twenty. The lumbar vertebrae (Fig. 4, *B*) have no ribs, the transverse processes are greatly elongated and usually attenuated, the broad spinous processes are directed obliquely forward, and the centra are markedly longer than those of the dorsal series.

The sacrum supports the pelvis, and is undifferentiated only in Cetacea and Sirenia, which have lost their hind limbs. Usually three to four vertebrae are fused to form a sacrum, but occasionally only two are involved, and more rarely as many as eight or nine may be included. The centra and neural arches, and often the spinous processes also, are fused together to make an immovable sacral segment, which is broadest in front, and tapers toward the tail.

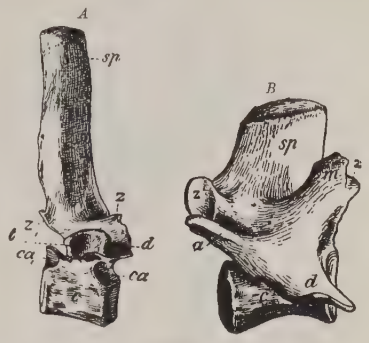


FIG. 4.

A, Second dorsal vertebra of the dog (lateral aspect). *B*, Second lumbar vertebra of the dog (lateral aspect). *c*, Centrum; *sp*, neural spine; *d*, diapophysis; *z*, anterior; *z'*, posterior zygapophysis; *m*, metapophysis; *a*, anapophysis; *t*, facet for the tuberculum; *ca*, facets for the capitulum.

The caudal vertebrae are the most variable of all in number and form. As a rule the most anterior ones have well-developed neural arches, spinous processes, transverse processes, zygapophyses, and occasionally V-shaped haemapophyses (chevron bones). Toward the rear modifications gradually decrease, the centra being more elongated, the arches and processes becoming vestigial or disappearing entirely, the last centra taking on a more or less cylindrical form.

The ribs are developed only in connection with the dorsal vertebrae, the more anterior or true ribs being attached distally by means of cartilaginous or imperfectly ossified costal cartilage to the sternum, while some of the posterior or floating ribs end free in the muscular wall of the chest. Each rib has two articulations, the tuberculum, which articulates with the transverse process, and the capitulum, which unites with the front of the centrum, or occasionally with the lower part of the neural arch. It often happens, also, that this articulation falls between two centra, so the capitulum is united to the centrum in front, as well as to the succeeding one. The sternum or breast bone is not a single element, but consists of a median row of flat, separate, bony pieces suturally united with each other.

The skull (Figs. 5, 6) of mammals is distinguished from that of fishes, amphibians, reptiles and birds, chiefly in the smaller number of constituent bones, in the fusion of the upper jaws to the cranium, in the suppression of the lower jaw supports, and direct connection of the dentary with the squamosal bone. The absence of a distinct quadrate and the presence of two occipital condyles are further characteristic of the mammalia. The form of the skull depends on the size of the brain, the development of the jaws, the presence of crests, bony protuberances, horns, etc., and shows tremendous variation in the different orders and families.

In the skull the bones bounding the brain cavity are called the cranial,

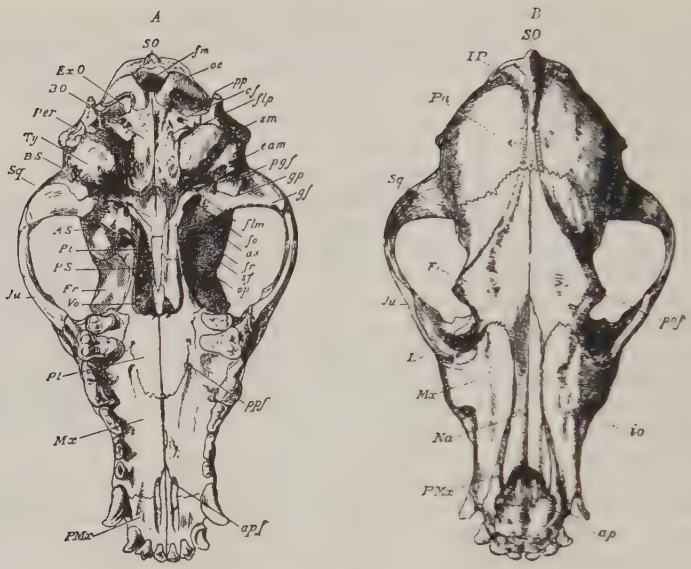


FIG. 5.

Skull of the dog (*Canis familiaris*). *A*, Palatal, and *B*, dorsal aspect. *so*, Supraoccipital; *pa*, parietal; *ip*, interparietal; *sq*, squamosal; *fr*, frontal; *l*, lachrymal; *ju*, jugal; *mx*, maxilla; *pmx*, premaxilla; *na*, nasal; *bo*, basioccipital; *exo*, exoccipital; *per*, periotic; *ty*, tympanic; *bs*, basisphenoid; *ps*, presphenoid; *as*, alisphenoid; *pt*, pterygoid; *vo*, vomer; *pl*, palatine; *pof*, postorbital process; *io*, infraorbital foramen; *oc*, occipital condyle; *pp*, paroccipital process; *gp*, postglenoid process; *gf*, articular surface for the lower jaw; *fm*, foramen magnum; *cf*, condyloid foramen; *flp*, foramen lacerum posterius; *sm*, stylomastoid foramen; *eam*, external auditory meatus; *pgf*, postglenoid foramen; *flm*, foramen lacerum medium; *fo*, foramen ovale; *as*, posterior opening of the alisphenoid canal; *fr*, foramen rotundum and anterior opening of the alisphenoid canal; *sf*, foramen lacerum anterius; *op*, foramen opticum; *ppf*, posterior palatal perforations; *apf* and *apf*, anterior palatal perforations. (After Flower.)

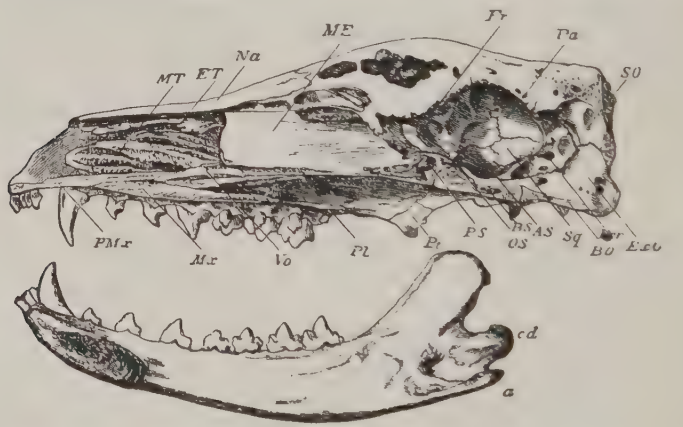


FIG. 6.

Thylacinus cynocephalus. Sagittal cross-section of skull and mandible. *so*, Supraoccipital; *exo*, exoccipital; *bo*, basioccipital; *per*, periotic; *bs*, basisphenoid; *ps*, presphenoid; *as*, alisphenoid; *os*, orbitosphenoid; *sq*, squamosal; *pa*, parietal; *fr*, frontal; *me*, mesethmoid; *na*, nasal; *et*, ethmoturbinal; *mt*, maxilloturbinal; *pmx*, premaxilla; *mx*, maxilla; *vo*, vomer; *pl*, palatine; *pt*, pterygoid; *cd*, condyle of the lower jaw; *a*, angle of the lower jaw. (After Flower.)

those bounding the mouth and nasal cavity the facial bones. The back of the cranium is pierced by the foramen magnum (*fm*), on either side of which is an exoccipital (*exo*) bone, carrying one of the occipital condyles. These two are connected by the unpaired supraoccipital (*so*) above and by the single basioccipital (*BO*) below. From the forward part of the exoccipital and separated from the occipital condyle by a deep groove, the paroccipital process (*processus paramastoideus, Pr. jugularis, pp*) projects downward, providing an attachment for muscles, and being especially developed in ungulates. The basioccipital extends well forward, making a considerable portion of the base of the cranium, and is perforated by a small circular condylar foramen (*cf*) for the hypoglossal nerve. In front of the basioccipital in the median line lies the basisphenoid (*BS*), in front of which is the presphenoid (*PS*), and in front of this in turn the vomer (*vo*). In the upper surface of the basisphenoid is a depression, bounded in front and behind by a ridge, making the so-called "Turk's saddle" (*sella turcica*), in which the pituitary body of the brain rests. From either side of the basisphenoid a wing-like plate of bone extends outward and upward, the alisphenoid (*AS, ala major*); and from the presphenoid a corresponding plate, the orbitosphenoid (*OS, ala minor*). The alisphenoid is usually perforated by three openings, of which the hindermost (*foramen ovale, fo*) provides an outlet for the third branch of the trigeminal nerve; the middle one (*canalis alisphenoideus, as*) the opening for the external carotid artery; and the front one (*foramen rotundum, fr*) the exit for the second branch of the trigeminal nerve. The orbitosphenoid has the foramen opticum (*op*) for the optic nerve, and between it and the alisphenoid occurs the *foramen lacerum anterius* for the third, fourth and sixth nerves and the first branch of the trigeminal.

The roof and upper part of the side of the cranium is formed by the parietals (*Pa*) behind, and the frontals (*Fr*). Frequently a small triangular bone, the interparietal (*IP*), occurs between the parietals and the supraoccipital. This may be paired, or may fuse to the parietals (Ungulata), or to the supraoccipital (Carnivora). The more or less vertical occipital surface (occiput) is in many cases bounded above by transverse crests (*crista occipitalis*) to which the neck muscles are attached.

The parietals are connected along the median line by an interlocking suture, and remain either entirely separate, or may fuse completely. Over the suture there is frequently a more or less prominent sagittal crest which usually divides in front into two diverging branches. The frontal bones occasionally fuse, and may, as in many ungulates, carry bony processes which support horns. As a rule, a postorbital process (*pof*) arises from the rear of the frontal and serves to bound the back of the orbit. In many ungulates, especially the horned ruminants, the entire frontal, often also the parietal, a part of the maxilla, and occasionally even the presphenoid, are filled with air chambers, while among the elephants almost all of the cranial or facial bones are swollen by the presence of unusually large air spaces. Extending from the frontal to the presphenoid and vomer, a more or less expanded vertical plate of bone, the mesethmoid, closes in the front of the brain cavity. This consists of an elongated median lamella (the *lamina perpendicularis* or *crista galli*), resting on the vomer, together with two lateral obliquely placed plates (*laminae cribrosae*) perforated by many apertures, through which the branches of the olfactory nerve pass when leaving the brain cavity. Toward the front the *lamina perpendicularis* almost always passes into a cartilaginous nasal septum.

Between the alisphenoid and supraoccipital bones lies the plate-like squamosal, bounded above by the parietal and often the back of the frontal, and filling in the lateral wall of the brain case. From the lower part of the bone arises a strong process (*processus zygomaticus*) corresponding to the squamosojugal arch of reptiles, which extends forward, carrying on its under surface a concave articulation (*fossa glenoidalis, gf*) for the reception of the condyle of the lower jaw. Behind this articular surface the posterior border is developed into the *processus postglenoidalis* (*gp*) projecting downward. The space between the exoccipital and the squamosal is filled in by the bones of the auditory capsule. In the cartilaginous mass forming the auditory capsule of mammals, ossification starts from three centres, corresponding to the prootic, opisthotic and epiotic of reptiles, but these all unite in the single dense periotic (*Per*), the inner part of which encloses the auditory labyrinth and inner ear, while the outer portion makes the mastoid process. In immature stages the tympanic bone consists of a simple bony ring around the ear opening, which condition is normal to the adult in marsupials and many insectivores; but, as a rule, the outer rim of the ring expands horizontally and forms the external passage or external auditory meatus (*eam*) for the ear. The lower margin of this opening is covered by a flattened bony plate which may be inflated, bladder-like, making the tympanic bulla (*Ty*), which may be hollow or may be filled with bony tissue.

In many cases the auditory bulla is formed from a separate element (*os bullae*, entotympanic), which may represent either a separated lamina of the periotic or an ossification in the wall of the tubo-tympanal duct. From the front of the tympanic occasionally projects downward and forward a pointed styloid process. In the opening between the periotic and tympanic bones, that is, the chamber bounded externally by the ear drum (tympanic membrane) and internally by the *fenestra ovalis*, lie the three minute ear bones, stirrup (*stapes*), the anvil (*incus*), and hammer (*malleus*). The foot-plate of the stapes lies in the fenestra ovalis of the periotic; the handle (manubrium) of the malleus is attached to the ear drum. In the anterior part of the tympanic bone is the opening of the Eustachian tube, which admits air from the pharynx to this middle-ear chamber; the internal carotid artery enters the brain case by various paths, sometimes passing through the tympanic chamber (many insectivores and lemurs), sometimes piercing the petrotympanic mass (*Tarsius*, higher primates), sometimes running along the inner side of the bulla (carnivores), sometimes entering through the *foramen lacerum medium* (certain lemuroids). The *foramen lacerum posterius* (*flp*) transmits the jugular vein and the ninth, tenth, and eleventh cranial nerves.

The appearance of the skull is largely dependent on the development of the facial bones; especially the maxilla (*mx*). This bone usually carries along its lower outer margin the teeth, and expands horizontally to make a large portion of the hard palate. From the back of the maxilla rises a strong process which is first directed outwardly, then backward, being connected by the jugal or malar (*Ju*) bone to the zygomatic process of the squamosal. Thus the zygomatic arch is completed, and makes the lower border of the orbit and of the temporal opening. In the anterior rim of the orbit, between the frontal, maxilla, and ethmoid, lies a small bone, the lachrymal (*La*), which is always perforated by the lachrymal canal. The front of the snout is formed by the two premaxillae (*pmx*), which usually carry some of the alveoli for teeth. The

top of the snout is covered by the two nasal bones (*Na*), which are set into the front of the frontals, bounded on the sides by the maxillae and usually premaxillae, and cover the olfactory chamber. In the olfactory chamber of all mammals, except whales and Sirenia, occur very thin, closely rolled, and fenestrated films of bone, covered with a mucous membrane and better developed in forms with an acute sense of smell. These are the turbinals, and are regarded as highly developed processes of the ethmoid bone. They are usually developed in several groups, those on the right and left being separated by the lamina perpendicularis of the ethmoid. The turbinals which occupy the upper portion of the olfactory cavity are termed the ethmoturbinals (*ET*), while those in the lower portion of the cavity, attached to the maxilla, are termed the maxilloturbinals (*MT*).

The back of the lower surface of the skull is composed of the basioccipital and basisphenoid bones. From the basisphenoid and alisphenoid there projects downward a short vertical plate of bone, the pterygoid (*pt*), which makes the sides of the posterior nasal passage, where the floor is formed by the soft palate. In front, the pterygoid unites with the back of the palatine (*pl*), the front of which bone expands to make a horizontal plate which, uniting with the corresponding plate of the maxilla, completes the hard palate, which is the floor of the olfactory chamber.

The lower jaw consists of two symmetrical and diverging halves, which meet in front along a rough surface (symphysis), and are either held together by connective tissue, or are rigidly fused in old age by bone. The upper or alveolar border is usually occupied by a row of teeth, the lower border is convex and thickened, rising in the region of the symphysis in front, and making an abrupt angle (*a*) behind, which may be prolonged into a process, or bent inward. Behind the last tooth the upper margin rises, as a rule, into a high compressed coronoid process, to which the temporal muscle is attached, while the powerful masseter muscle is provided with an attachment in the shape of a shallow depression on the outer side of the coronoid.

The posterior margin of the ascending portion of the lower jaw is expanded just above the angle to make a thickened convex articular condyle (*cd*), which fits the glenoid fossa on the squamosal, and may be elongated transversely or longitudinally. A wide alveolar canal extends the length of the lower jaw, and carries the mandibular artery and nerve from which arise numerous branches to the various teeth. On the inner side of either jaw may occur a shallow groove (*sulcus mylohyoideus*), which is especially characteristic of marsupials.

The brain cavity in mammals is markedly larger than in the other classes of vertebrates. In general the different orders show a measurable increase in the size and structure of the brain, so much so that Owen used this as a basis of his systematic arrangement. The fact first observed by Marsh, that size of the brain is universally smaller among Eocene genera than among the members of the same families in later Tertiary and later times, is very noteworthy; and indeed the brain cavity in the skulls of some of the giant Eocene amblypods can be contained within the medullary canal.

Development and Morphology of the Skull.—As in reptiles and birds, the skull consists of a primordial portion preformed in cartilage, and a secondary portion, the bones of which develop in membranes. The various bones are at

first all widely separated, arising from special centres of ossification, and gradually expand until they meet, and are either connected by sutures or are fused together. Thus the form and structure of the skull depend on the manner of growth and union of the component bones; and with reference to the ontogenetic or phylogenetic succession, certain conditions are termed primitive, and others more or less modified or specialised. Some of these differences are indicated in the following table:—

Primitive Characters.	Specialised Characters.
Bones united by sutures.	Bones fused together.
Brain cavity small and narrow.	Brain cavity large, wide, expanded.
Skull low, profile almost straight.	Forehead region arched, or rising markedly.
Facial portion of skull elongated.	Facial portion of skull short or retreating, or snout greatly prolonged.
Nasal bones long, nostrils directed forward.	Nasal bones short or vestigial; nostrils far back or directed upward.
Upper jaw low.	Upper jaw high.
Zygomatic arch complete.	Zygomatic arch interrupted or vestigial.
Orbit open behind, confluent with temporal opening.	Orbit closed behind.
Frontals and presphenoid dense or with small air spaces.	Frontals, and often adjacent bones, and the base of the cranium, filled with air spaces.
Bones on roof of skull smooth.	Parietal, occipital or frontal bones having prominent crests, protuberances, horns or antlers.
Tympanic ring-like open below, free.	Tympanic closed below, or with expanded bulla; with an auditory meatus; and fused to the periotic.
Articular facet for lower jaw shallow, with a postglenoid process behind.	Articular facet deep, and bounded by strong ridges, postglenoid process wanting.
Halves of lower jaw united at the symphysis by ligaments.	Halves of lower jaw co-ossified at symphysis.

The pectoral arch, in comparison with that of lower vertebrates, has sustained considerable reduction, consisting, as it often does, of simply a scapula, and, in such forms as use the fore limbs in climbing or for prehension, of a clavicle. The coracoid and precoracoid are present only in monotremes, being in all other forms greatly reduced and fused with the scapula as a process.

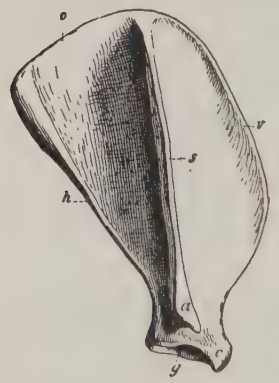


FIG. 7.

Right scapula of the dog. *s*, Scapular crest; *a*, acromion; *c*, coracoid process; *g*, articular surface; *v*, anterior (coracoid) margin; *h*, posterior (glenoid) margin; *o*, superior margin.

The scapula (Fig. 7) is a rather large, rounded, triangular bone, on the outer side of which is a prominent crest (*spina* or *crista scapulae*, *s*) dividing it into an anterior and posterior fossa. As a rule the anterior end of the crest projects as an elongated and bent acromion process (*a*). The lower and narrower end is expanded to form a shallow cup, the glenoid fossa (*g*), for the reception of the head of the humerus. On the extreme end is a short coracoid process (*c*), which ossifies from a separate centre, and is united during adolescence by a suture only, finally fusing completely with the scapula.

The clavicle is a paired, slender, cylindrical, slightly curved bone, extending from the sternum to the acromion process of the scapula. It is

lacking in Cetacea, Sirenia, all recent Ungulata, and in most Carnivora; but it is very stout in burrowing mammals.

On the upper articular end of the humerus (Fig. 8) is a rounded head, adjacent to which are two prominent processes for muscular attachments, the greater and the lesser tuberosity, separated from each other by the bicipital groove (*bg*). From the greater tuberosity, and along the outer face of the humerus, runs the wide rough deltoid ridge (*d*), extending far down the shaft. The distal or lower end of this bone is transversely expanded, and carries a pulley-like articular surface (trochlea), which is divided either by a groove or by a raised rim (*crista intertrochlearis*) into a small radial (*ar*) and an ulnar (*au*) articular facet. On either side of the trochlea projects a spur, the outer being the external condyle (*ec*), the inner the internal condyle (*ic*). Just above the latter the humerus of many primitive mammals is perforated by an entepicondylar (*ent*) foramen, allowing the passage of the median nerve and the brachial artery. Above the trochlea the humerus is excavated on the back by a shallow or deep pit which receives the olecranon process of the ulna, and may perforate the bone. In youth the upper and lower articular ends (epiphyses) are separate from the shaft.

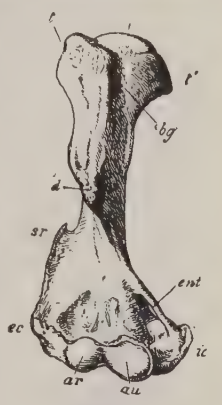


FIG. 8.

Right humerus of the wombat (*Phascolomys wombatus*), anterior view. *c*, Upper articular surface (caput); *t*, tuberculum majus; *t*, tuberculum minus; *bg*, bicipital groove; *d*, deltoid process; *sr*, crista supinatoria; *ent*, entepicondylar foramen; *ec*, outer, *ic*, inner articular surfaces; *ar*, radial, *au*, ulnar facets.

FIG. 9.

A, Left radius of the dog (anterior aspect). *c*, Upper, *g*, lower articular surface; *ps*, processus styloideus; *e*, epiphysis. *B*, Left ulna of the dog (anterior aspect). *ol*, Olecranon; *fs*, fossa sigmoidea; *fl*, fossa lunaris; *c*, capitulum; *e*, epiphysis.

The forearm (Fig. 9) consists of two bones, radius and ulna. In such mammals as use the fore-limb for climbing or grasping, both bones have developed a rotating articulation on the proximal end. In most mammals the ulna is situated behind the radius. In the more specialised ungulates the lower end of the ulna is lost, and the upper part fused to the back of the radius.

The upper end of the radius has a shallow, oval, articular depression; the shaft is somewhat compressed, and the lower end expanded and provided with a short, sharp, styloid process (*ps*) bounding the inner side of the articular surfaces. On the upper end of the ulna is a powerful, four-sided, olecranon process (*ol*), in front of which is the deep sigmoid notch or articulation (*fs*). In most mammals the lower or distal end of the ulna is narrow, and has a convex articular surface which is bounded externally by its styloid process.

The carpus or wrist (Fig. 10) consists among all mammals of two rows of small bones, between which, among primitive forms, a tiny centrale may be present. These bones are as follows:—

Mammalian Carpus.		Reptilian Carpus.
Scaphoid	=	Radiale.
Lunar	=	Intermedium.
Cuneiform	=	Ulnare.
Pisiform	=	Pisiform.
Centrale	=	Centrale.
Trapezium	=	Carpale I.
Trapezoid	=	Carpale II.
Magnum	=	Carpale III.
Unciform	=	Carpale IV.[1]

Of the above the pisiform is a bone, which is by some considered the representative of a sixth finger, by others a sesamoid bone. The pisiform is well represented in Permian reptiles and amphibians. The centrale often fuses with the scaphoid. The second centrale of reptiles is apparently lost in mammals. In the primitive carpus all these bones remain separate, the arrangement being more alternate than serial. Where weight has to be supported, the carpus is usually rearranged in various ways. For the the upper row becomes more compact, the lunar and scaphoid often fusing; while fusions of adjacent bones take place in the lower row also. Another mode of strengthening is seen among ungulates, where the distal row of bones is rearranged so as to alternate with the upper row, and thus make a more compact joint. The same result is attained by the expansion of a wrist bone, for example the magnum (Fig. 10, C). The lateral expansion of a distal carpal bone, in connection with the loss of the first digit, often causes the entire suppression of the trapezium.

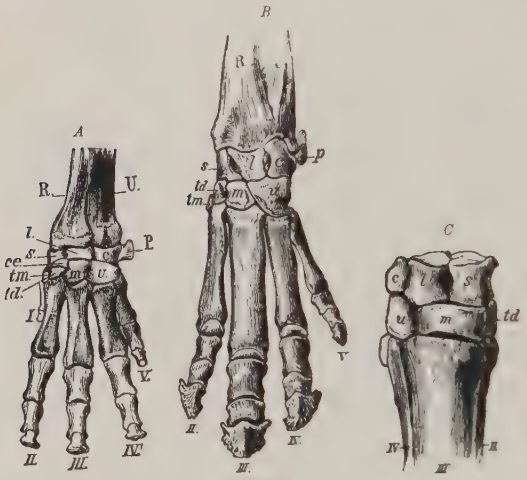


FIG. 10.

A, Left manus of *Procavia* (*Dendrohyrax*) *arborea*. *B*, *Tapirus Americanus*. *C*, Right manus of the horse. *R*, Radius; *U*, ulna; *s*, scaphoid; *l*, lunar; *c*, cuneiform; *p*, pisiform; *ce*, centrale; *tm*, trapezium; *td*, trapezoid; *m*, magnum; *u*, unciform; *I.-V.*, digits.

Beyond the carpals come the metacarpals, one opposite each carpal, except the unciform which supports metacarpals *IV.* and *V.* Originally the articular ends of the metacarpals made an even row, but individual bones have pressed into the carpal row making an uneven but much stronger articulation. The distal rounded articular facets are often divided by a sharp ridge into two surfaces.

Of the five digits the first, inner, or radial one is often termed the thumb (pollex). With the exception of whales, no mammal has more than three phalanges to each digit. The first and fifth digits often lack one or two joints,

[1] Carpale V. is much reduced in many early reptiles, and probably disappeared in the mammalian manus.

and among edentates two joints may be fused. Among the bats the metacarpals and phalanges are enormously elongated to furnish supports for the wing-membrane. The terminal phalanges vary greatly and are enclosed or protected in front by nails, hoofs or claws. Often, on the palmar side of the hand, opposite the articulation between the metacarpus and first phalanx, paired semilunar, sesamoid bones are developed in the connective tissue of the region.

The pelvis (Fig. 11) of either side consists of three bones which all meet in the articular cup (acetabulum) for the femur, the three bones, ilium (*il*), ischium (*is*), and pubis (*pb*), being independent in youth but usually fusing in the adult to make the innominate bone. The two innominate bones meet in the median ventral line, making the symphysis. The pubis and ischium expand along this symphysis, finally meeting and enclosing between them the obturator foramen (*fo*), which is in life closed with connective tissue and muscle.

The thigh bone or femur (Fig. 12) is usually a long cylindrical bone, the ball-like head of which is separated from the shaft proper by a constricted neck. Opposite the head, on the outer and back side of the femur, projects the greater trochanter ($tr.^1$) for muscular attachments, and separated off by a shallow to deep depression, the digital fossa. On the front and inner side of the bone, just below the head, occurs the smaller conical lesser trochanter ($tr.^2$). A third trochanter may occur on the hind border of the shaft below the greater trochanter, and at some distance from it; it is present in many primitive placentals, including many ungulates, rodents, insectivores and edentates. The distal end of the femur is greatly thickened, narrow in front, but expanding behind, with two rounded articular facets, the ectocondyle (*ca*) and entocondyle (*ci*), separated by the intercondylar groove (*f*), and each bounded externally by a prominent ridge.

FIG. 11.

Right innominate bone of the dog, seen from in front. *il*, Ilium; *pb*, pubis; *is*, ischium; *a*, acetabulum; *fo*, foramen obturatorium; *s*, symphysis.

FIG. 12.

Right femur of the dog (posterior aspect). *c*, Condyle; $tr.^1$, larger, and $tr.^2$, smaller trochanter; *ci*, inner articular surface (entocondylus); *ca*, outer articular surface; *f*, fossa intercondyloidea.

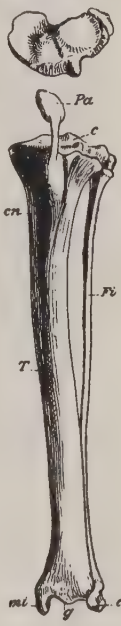


FIG. 13.

Left tibia (*t*) and fibula (*fi*) together with patella (*pa*) of the dog, seen from in front. *c*, Upper articular surface; *g*, lower articular surface of the tibia; *cn*, procnemial ridge; *mi*, malleus internus; *co*, lower facet of the fibula.

The thick upper end of the tibia (Fig. 13) forms a triangular, slightly depressed articular facet (*c*), separated into two surfaces by a median bifid

ridge. The shaft is flattened on the back side. The upper end of the anterior surface is raised in a narrow ridge, the procnemial crest (*cn*), while the lower end is expanded on a broad articular facet, which latter may be divided into two portions by a median ridge, while the inner boundary is also raised to make the malleolus internus (*mi*). The fibula (*fi*) is always a slender bone, the lower end (*co*) of which is often prolonged into a process corresponding to the malleolus internus, and resting on the outer surface of the astragalus or calcaneum. In front of the articulation between the femur and the tibia is a small patella (*Pa*) connected by ligaments with the tibia.

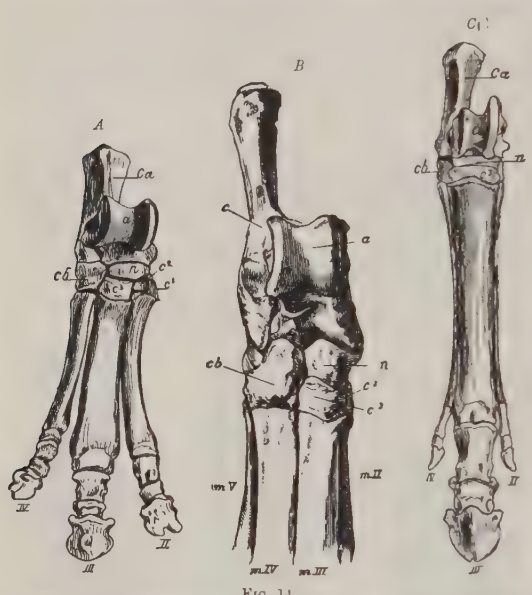


FIG. 14.

Right pes of *Palaeotherium* (*A*), of the pig (*B*), and of *Hipparion* (*C*). *ca* and *c*, Calcaneum; *a*, astragalus; *n*, navicular; *cb*, cuboid; *c¹*, *c²*, *c³*, cuneiform, primum, secundum, tertium; *m*, metatarsals: *II.-V.*, second to fifth digits.

As in the case of the carpus, the ankle or tarsus (Fig. 14) consists of two rows of bones, between which there is always a well-developed centrale or navicular. The upper row consists of the astragalus (= tibiale plus intermedium[1]) on the inner side;

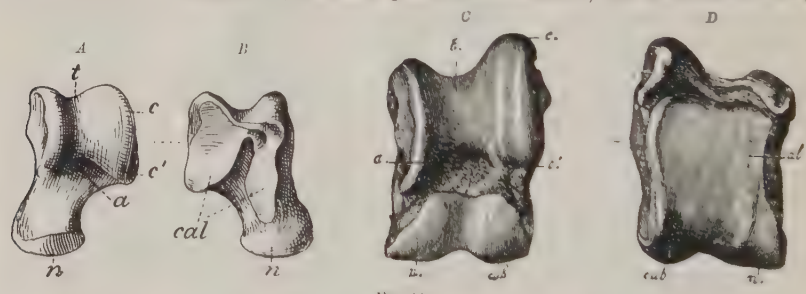


FIG. 15.

Left astragalus of the dog, *A* from front and above, *B* from behind and below; and left astragalus of a large ruminant (*Helladotherium*), *C* from front and above, *D* from behind and below, half nat. size (after Gaudry). *t*, Tibial facet (trochlea); *c*, *c'*, lateral border for articulation with calcaneum; *cal*, facet for calcaneum; *a*, fossa for reception of lower border of tibia; *n*, facet for navicular; *cub*, facet for cuboid.

and the calcaneum (= fibulare) on the outer side. The astragalus articulates with the tibia to make the ankle joint. The anterior and upper articular

[1] The astragalus is more probably homologous with the enlarged intermedium, as in Permian reptiles, the tibiale having been lost.

facet is, among the heavy ungulates (Amblypoda and Proboscidea), almost flat; but as a rule there are two prominent ridges separated by a deep groove.

The distal portion of the astragalus may be prolonged, making a neck, the end either resting by a flat or slightly arched articular facet on the navicular, or presenting a broad arched roller facet to the navicular, cuboid and calcaneum (Fig. 15, *c*). On the posterior face of the astragalus lie one or two facets for the calcaneum, and one for the cuboid. In primitive forms there occurs a foramen above the proximal facet.

The calcaneum (Fig. 16) is an elongated angular bone, the rear of which is prolonged in an abbreviated stem (*tuber calcis, tc*), which in plantigrade animals rests on the ground and makes the heel, while in digitigrade types it is raised and directed obliquely upward and backward. Distally the calcaneum comes in contact with the cuboid, and anteriorly with the upper part of the astragalus. A process (sustentaculum) on the inner side bounds the sustentacular facet (*as*) for the astragalus; while on the opposite outer side occurs the peroneal facet (*p'*); and occasionally there is also a facet for the fibula (*p*). The cuboid is an irregular four-sided bone, somewhat higher than broad. The navicular extends over the three adjacent cuneiform bones.

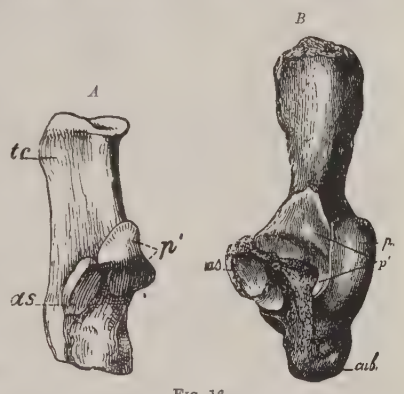


FIG. 16.

Left calcaneum of the dog (*A*) and of *Macrauchenia* (*B*). *tc*, Tuber calcis; *as*, sustentacular facet for astragalus; *p'*, outer or peroneal facet for astragalus; *cub* distal facet for cuboid; *p*, facet for fibula.

The metatarsals (*m*) correspond in general with the metacarpals, though their proximal articular ends are usually flattened and pressed close against the tarsalia, the articulations being usually about on a level. But the fourth and fifth (*m.IV.* and *V.*) metatarsals articulate with the cuboid, the others each articulating with a single tarsal bone. By the development of *m.III.* and *IV.* the same reductions may take place on the hind- as on the fore-foot, the first or great toe (hallux) being the first lost, then the fifth, followed by the second, and in the most extreme cases (horse) the fourth may also be sacrificed. Among ruminants *m.III.* and *IV.* fuse as in the fore-limb to make the cannon bone.

The phalanges and sesamoids of the hind-foot differ as a rule but slightly in number, size and form from those of the front foot.

Mammalian Tarsus.		Reptilian Tarsus.
Astragalus	=	Intermedium.
Calcaneum	=	Fibulare.
Navicular	=	Centrale.
Cuboid	=	Tarsale IV.
Entocuneiform	=	Tarsale I.
Mesocuneiform	=	Tarsale II.
Ectocuneiform	=	Tarsale III.

In general the development of the limb depends closely on the modifications and habits of the animal. As in many cases the limbs are used exclusively for

locomotion, for running and grasping, for climbing and digging, for flying or for swimming, so for each of these adaptations special modifications are developed; and as a result it often happens that animals of very distant relationships exhibit similar structural modifications when subjected to similar conditions of environment. These facts indicate a plasticity in the entire organism, including the skeleton, which is clearly observable among the various representatives of a group as they pass from one phylogenetic stage to another in the course of geological history. The study of the changes in the mammalian skeleton during its phyletic development, or so-called "kinetogenesis," has been especially fostered by Cope and Osborn, whose guiding principles are but slightly modified from the evolutionary views of Lamarck.[1] More recently, however, H. F. Osborn has contested Lamarck's theory.

With the study of the skeleton, that of the dentition of mammals is of the greatest practical importance for systematic purposes, for not only do the teeth show an extraordinary amount of variation, but they stand in the closest relation to food habits and skeletal structure. The teeth have, therefore, from earliest times been especially valued for classificatory purposes, and especially in Palaeontology, on account of their resistance to destructive agencies during fossilisation.[2]

The teeth (Fig. 17) of most mammals consist of enamel, dentine and cement, and enclose a pulp cavity filled with cellular tissue, blood-vessels and nerves. Vasodentine is found only among the Edentata. The cement (*crusta petrosa*, *c*) forms as a rule only the thin crust over the root; but it may form a more or less thick crust round the crown, and sometimes fills pits and valleys between the ridges on the top of the crown. The pulp cavity (*p*) occupies a large space in the crown and root or roots of young teeth. In such young teeth the openings at the base of each root are wide, but as they mature, these openings are greatly narrowed. When the teeth remain without roots and the pulp gives rise to continuous growth, they are said to have persistent pulps. Teeth with low crowns, well-developed and narrowed pulp cavities, are termed *brachyodont*; while such as are of high cylindrical or prismatic form, with an open pulp cavity, with or without roots, are called *hypsodont*.

The form of mammalian teeth is very largely determined by their

[1] Literature: *Cope, E. D.*, The Origin of the foot structures of the Ungulata. Journ. Acad. Nat. Sci. Philad., 1874.—On the effect of impact and strains on the feet of Mammalia. Amer. Naturalist, 1881. —The mechanical causes of the development of the hard parts of the Mammalia. Journ. Morph., 1889.—Primary factors of organic evolution, 1896.—*Osborn, H. F.*, The evolution of the ungulate foot. Trans. Amer. Phil. Soc., 1889.—*Schlosser, M.*, Über die Modifikationen des Extremitätenskeletes bei den einzelnen Säugetierstämmen. Biol. Centralblatt, 1890.—*Scott, W. B.*, On some of the factors of the evolution of Mammalia. Journ. Morph., 1891.

[2] *Ameghino, F.*, Sur l'évolution des dents des mammifères. Bol. Acad. Nacion. Cienc. Cordoba, 1896.—Recherches de morphologie phylogénétique sur les molaires supérieures des ongules. Anal. Mus. Nac. Buenos Aires, 1904.—*Cope, E. D.*, The mechanical causes of the development of the hard parts of the mammalia. Journ. Morph., 1889.—*Flower, W. H.*, Remarks on the homologies and notation of the teeth of the Mammalia. Journ. Anat. Physiol., 1869.—*Kowalevsky, W.*, Anthracotherium. Palaeontogr., 1874, Bd. XXII.—*Osborn, H. F.*, Evolution of mammalian molars to and from the tritubercular type. Amer. Naturalist, 1888.—The same, New York, 1907.—*Owen, R.*, Odontography. London, 1840-45.—*Schlosser, M.*, Biol. Centralbl., 1890.—*Scott, W. B.*, The evolution of the premolar teeth in the Mammalia. Proc. Acad. Nat. Sci. Philad., 1892.—*Wortman, J. L.*, The comparative anatomy of the teeth of the Vertebrata. Washington, 1886. For a critique of the Cope-Osborn theory of the evolution of the molars, see *Gregory, W. K.*, in Bull. Amer. Mus. Nat. Hist., 1910, pp. 184-194, and *ibid.*, 1916. Also *Gidley, J. W.*, Evidence bearing on Tooth-Cusp Development. Proc. Washington Acad. Sci., 1906, vol. viii. pp. 91-210.

physiological function. For grasping and holding the prey, simple and conical teeth serve best; if used as weapons or to remove obstacles, they are elongated and project out in front of the mouth, or become modified into tusks. If the food is varied and requires an apparatus for grinding it, then division of labour and specialisation take place. Certain teeth function exclusively for grasping and holding the food, while others tear, cut, crush and grind it; and as these processes are generally carried on in different parts of the mouth, the anterior teeth are differently formed from those more remotely situated in the mouth.

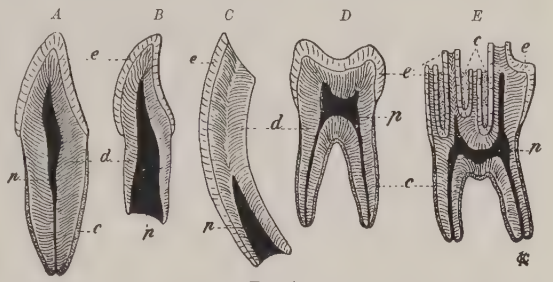


FIG. 17.

Vertical sections of various teeth, namely, a full-grown single-rooted incisor (*A*), an immature incisor with widely open pulp cavity (*B*), an incisor of a rodent, with the front face enamelled and the pulp persistently growing (*C*), a molar tooth of man, with a low broad crown (*D*), and a molar tooth of an ox, with a deep crown and folds of enamel filled with cement (*E*). *e*, Enamel; *d*, dentine; *c*, cement; *p*, pulp cavity.

Teeth are wanting only when the food requires no comminution, as among whales and ant-eaters. Uniformity of dental structure (homodont dentition), resembling that of lower vertebrates, also occurs secondarily only when, as in marine forms, the teeth are used solely for seizing and holding the prey. Most mammals have a differentiated or heterodont dentition, the teeth of either side of a jaw being repeated symmetrically on the other side. The teeth situated in the premaxilla and in the front part of the lower jaw are termed *incisors* (*I*). Just behind the upper incisor and directly behind the suture between the premaxilla and maxilla is placed the conical single- (seldom two-) rooted canine (*C*), corresponding to which in the lower jaw is the lower canine. Behind the canine comes the series of molars or cheek-teeth, the more anterior of which, being usually simpler, are termed *premolars* (*P*), and the posterior the *molars* (*M*). If all these kinds of teeth are present the dentition is termed complete; and incomplete if any are lacking.

Among toothed whales, Sirenia and most edentates, the first set of very simple teeth continue in use throughout life. These comparatively few monophyodont forms stand in marked contrast to the great majority of diphyodont mammals which have two sets of teeth. The replacement of teeth, however, occurs but once during life. The first set is termed milk or *deciduous* teeth, and this is replaced by the second or *permanent* set. The milk teeth are also differentiated as incisors, canines and molars, the first two types corresponding to their successors in number and form, while a less number of milk molars occur, and these correspond in form rather to the molars than to the permanent premolars which replace them. There are no teeth in the milk dentition which precede the molars of the permanent dentition, for the so-called milk molars are replaced by the permanent premolars. The first post-canine milk tooth is never replaced and is usually regarded as the first premolar of the adult series (Leche). Among marsupials usually only the last milk molar is replaced, the anterior milk molars may have been lost. The dental succession is apparently being lost, for among all the orders it takes place now at a

much earlier period than in the members of the same families in early Tertiary times.

The number of teeth in monophyodont mammals is highly variable, following no fixed law. Primitive diphyodont mammals have 44 teeth in the permanent dentition, the dental formula being $I\frac{3}{3}$, $C\frac{1}{1}$, $P\frac{4}{4}$, $M\frac{3}{3}$. In the milk dentition the formula is $DI\frac{3}{3}$, $DC\frac{1}{1}$, $DM\frac{3}{3}$. Among diphyodont forms not only are the teeth of the right and left jaws symmetrically arranged, but there prevails a definite law as to the number and position of the different teeth. In almost every order and family of mammals those occurring in the more recent geological formations have fewer teeth than the early representatives of the order or family; while an increase above the normal number rarely occurs in any of the diphyodont mammals. The reduction almost invariably begins at one or the other end of any series of teeth, for instance with the last or first incisor, or with the first premolar, or the last molar, and proceeds from that point either forward or backward.[1]

The form and size of the different teeth depend on their function, position and nourishment. One can safely say that the conical, single-rooted tooth set at regular intervals along the jaw was the primitive type of the ancestral mammal reptiles, and the canine tooth represents the least deviation from this type. The canines are generally conical, single-pointed teeth (two-rooted only among certain marsupials and insectivores), used chiefly for tearing and grasping the food, and therefore chiefly developed among carnivores.

The incisors are used as a rule for biting off and grasping the food: if for grasping, they are conical and similar to canines; if for biting, the crown is compressed from front to back, making a cutting chisel- or gouge-like edge. In all cases they are single-rooted. In case the incisors serve for special functions, they become modified accordingly. Thus, those employed for gnawing become large, slightly curved, sharp, usually long and very frequently with enamel only on the anterior surface. The strong, conical upper incisors of the Sirenia are adapted for uprooting aquatic plants; the massive tusks, with persistent pulp, and either entirely lacking enamel or having it in bands as in the case of the proboscidians and of narwhals, serve as weapons, or for the removal of obstacles, and the like. With increase in size and specialisation of the incisors a decrease in number is apt to occur. Complete lack of these is found in the Edentata; ruminants lose the upper incisors entirely, and most proboscidians the lower ones.

The cheek-teeth serve by far the greatest variety of functions, and accordingly they show the greatest amount of specialisation. As a rule, they display a tendency for the crown to become enlarged and provided with tubercles, cusps or ridges for the purpose of masticating food. Carnivores and insectivores use their cheek-teeth entirely for cutting up their prey and crushing the bones. Teeth with narrow, elongated, pointed and multi-

[1] In making the abbreviated dental formula, the teeth of a single jaw only are used, the expression, for example, of the tapir's dentition being thus written:—

A, permanent dentition, $i\frac{3}{3}$, $c\frac{1}{1}$, $p\frac{4}{4}$, $m\frac{3}{3} = \frac{11}{1} \times 2 = 44$,
or shorter, $\frac{3}{3}$, $\frac{1}{1}$, $\frac{4}{4}$, $\frac{3}{3}$.
B, milk or deciduous dentition, $di\frac{3}{3}$, $dc\frac{1}{1}$, $dm\frac{3}{3}$, $= \frac{7}{1} \times 2 = 28$,
or shorter $D = \frac{3}{3}$, $\frac{1}{1}$, $\frac{3}{3}$.

When reductions have occurred they appear in the formula, as for example in the case of the goat:—

$\frac{0}{3}$, $\frac{0}{1}$, $\frac{3}{3}$, $\frac{3}{3} = 32$.

tubercular crowns are used for the former purpose, whereas those with broad crowns provided with pointed cusps serve the latter purpose. Insectivores and carnivores have, therefore, cutting, multi-tubercular (secodont) crowns on the cheek-teeth which are very effective, and function as shears. The upper teeth override the lower, and close outside them. Animals of omnivorous diet have a bunodont dentition; that is, the low crowns of the cheek-teeth are enlarged and provided with conical cusps. The articulation of the lower jaw, as in the case of insectivores and carnivores, is vertical (orthal), and the condyle is transversely directed.

The cheek-teeth of herbivorous mammals reach the highest stage of specialisation. Here also we find the common tendency to enlarge these teeth

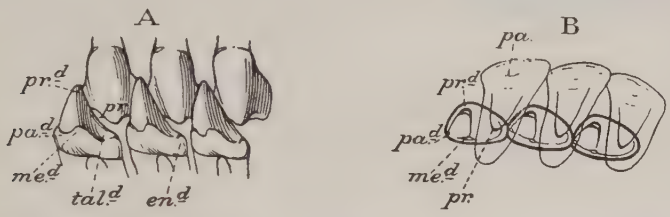


FIG. 18.

Hypothetical development of the tritubercular tooth pattern. *A*, Inner aspect of upper and lower molars. *B*, Upper and lower molars superimposed. *pr*, protocone; *pa*, paracone; *prd*, protoconid; *pad*, paraconid; *med*, metaconid; *end*, entoconid; *tald*, talonid. (After Gregory.)

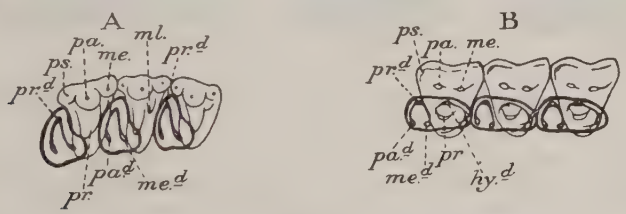


FIG. 19.

A, *Dryolestes*. Upper Jurassic. Lower molar still tritubercular but without hypoconid; upper molar tritubercular with parastyle. *B*, *Triisodon*. Lower Eocene. Lower molars tuberculo-sectorial. Both tooth rows superimposed. *pr*, *pa*, *prd*, *pad*, *med*, *end*, as in Fig. 18; *me*, metacone; *ps*, parastyle; *ml*, metaconule; *hyd*, hypoconid. (After Gregory.)

in length and breadth, and to provide them with cusps for the grinding of the food. The conical cusps of the original bunodont tooth become V-shaped, in that two converging outer ridges are formed. Either by the pronounced development of the branches of the V-shaped ridges, or by the compression of their extremities, or again by the union of the two cusps by a straight or curved transverse ridge, a complicated lophodont crown, with many crests, ensues. The motion of the lower jaw has an especial influence on the formation and direction of these ridges. If the mandible moves extero-interiorly (ectal) in the chewing process, as is the case with most herbivorous ungulates, or intero-exteriorly (ental), the V-shaped crests are arranged longitudinally one behind the other, and the borders of the cusps as well as the transverse ridges are placed at right angles to these. Very frequently the apices of the V-shaped ridges are worn down to form crescents (selenodont ridges). If the lower jaw moves in an antero-posterior plane (proal mastication),

as in most rodents, and the condyle moves in a longitudinal depression of the squamosal bone, the ridges are placed transversely to the longitudinal axis of the teeth. This arrangement is found, also, in the Proboscidia, where the mandible moves antero-posteriorly (palinal). A bunodont as well as a lophodont tooth may become very complicated, by a folding of the enamel-ridges, by the formation of spur-like processes, by the insertion of adjoining and secondary cusps, by the development of cingula, and finally by the addition of cusps and ridges on the posterior surface. As a rule, the upper cheek-teeth, which extend over those of the lower jaw, are broader than the latter; these, however, become enlarged antero-posteriorly.

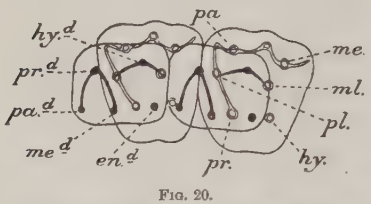


FIG. 20.

Development of the molars of Ungulata. Upper and lower molars superimposed. *pr*, *pa*, *me*, *ml*, *prd*, *pad*, *med*, *end*, *hyd*, as in Fig. 19; *hy*, hypocone; *pl*, protoconule. (After Osborn.)

It has been argued with much ingenuity by Cope and Osborn that the multitudinous modifications of the molar teeth have been derived from the single

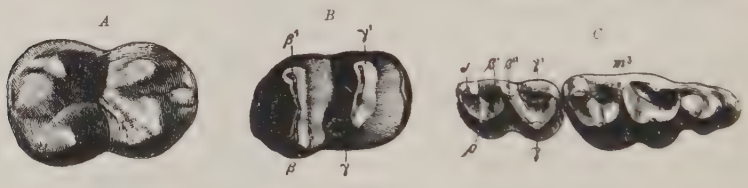


FIG. 21.

A, *Elotherium*, lower molar bunodont. *B*, *Hyrachyus*, lower molar lophodont. *C*, *Anoplotherium*, ectocones crescent-shaped; endocones conical. m^3 with a supernumerary crescent.

cone characterising reptilian teeth. This primitive *haplodont* tooth gives rise to the *protodont* type, as lateral cusps are formed and the root begins to divide. When the lateral cusps approximate the principal cone in size, there may be distinguished either the *triconodont* tooth, with three cones in a row, or the *tritubercular*, which has the lateral cones displaced to one side and alternating with the principal cone. In both types the root is divided.

Triconodont teeth are limited to but a few groups of mammals, and are not of especial significance for tracing the evolutionary history of molars. Much more important for this purpose is the tritubercular type of dentition, the earliest manifestations of which are perceived among certain Cynodontia, the reptile-like precursors of mammals.

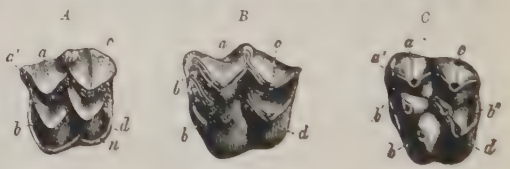


FIG. 22.

Inferior aspect of four-, five-, and six-cusped upper molars. *A*, *Protadrenotherium*. *B*, *Anoplotherium*. *C*, *Lophiotherium*.

In the tritubercular dentition the so-called *trigons* of the upper, and *trigonids* of the lower, jaw were effective organs so long as the mammals developing them remained of small size and subsisted chiefly on insects. With the gradual increase in size of body and change to a carnivorous or mixed diet, stronger

molars became necessary ; and this requirement was effected by the introduction in the lower jaw of a usually triconid *talonid* to function as antagonist against the principal cone of the corresponding upper molar. At the same time, in the upper dentition, the two outer cones became larger, and, in addition, two

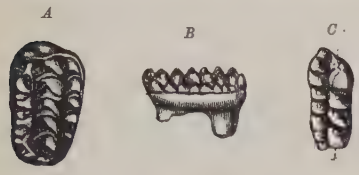


Fig. 23.

Multitubercular molars of Allotheria. *A*, *B*, Upper tooth of *Cimolomys*. *C*, Lower tooth of *Cimolomys*. 3/1. (After Marsh.)

Fig. 24.

Polylophodont molar of *Stegodon*. About 1/2.

minor cusps were formed. Of these latter, the hindermost often became metamorphosed, when the diet was mixed, into an intermediate cusp, although this may also arise independently as a growth from the cingulum.

The following nomenclature is applied to the different elements of molars having four or five cusps :

A. Upper Tritubercular Molars.

Anterior inner cone or cusp	protocone	pr.
Posterior „ „ „	hypocone	hy.
Anterior outer „ „	paracone	pa.
Posterior „ „ „	metacone	me.
Anterior intermediate cone or cusp	protoconule	pl.
Posterior „ „ „	metaconule	ml.
Antero-external peripheral cusp	parastyle	ps.
Medio-external cusp	mesostyle	ms.
Postero-external cusp	metastyle	mts.

B. Lower Tritubercular-Sectorial Molars.

Anterior outer cone or cusp	protoconid	prd.
Posterior „ „ „	hypoconid	hyd.
Anterior unpaired cone	paraconid	pad.
Posterior „	hypoconulid	hyld.
Anterior inner cone or cusp	metaconid	med.
Posterior „ „ „	entoconid	end.

The classification of mammals has been very greatly influenced by the discovery of numerous transitional fossil forms, since genera and even families and orders of recent forms, which apparently are not allied, become interrelated by means of fossil ancestors, and the presumably well-defined limits between them become less distinct. On the other hand, fossil forms have been found which require the establishment of new families, and even, in some cases, a new order, to accommodate genera absolutely unique among mammals. In most cases, the evolutionary history of single genera, families and orders can be traced with more certainty among mammals than in any other class of

vertebrates. In no other division of the animal kingdom have we as much material at our disposal for the reconstruction of the genealogical succession.

Concerning the origin of the *Mammalia*, birds and modern types of fishes cannot be considered as standing in the direct line of descent. The *Amphibia*, too, from which Huxley thought the *Mammalia* are descended, are more distantly removed than the *Reptilia*. Among these the *Theriodontia* are so like the mammals that Owen and Cope considered them as true ancestors. According to the latest researches of Broom, Watson, and others, it is a well-established fact that the mammals are closely related to or derived from the theriodonts.

The *Mammalia* are commonly divided into two subclasses, depending upon the nature of their embryological development; namely, the *Eplacentalia* and the *Placentalia*. The former include the orders *Monotremata* and *Marsupialia*; the latter, the orders *Insectivora* (including *Tillodontia*), *Chiroptera*, *Carnivora*, *Cetacea*, *Edentata*, *Rodentia*, *Ungulata*, *Notoungulata*, *Subungulata* (including *Sirenia*) and the *Primates*.

Subclass A. EPLACENTALIA.

Embryonic development without placenta.

Order I. MONOTREMATA[1] Bonaparte.

(*Ornithodelphia* Blainville.)

Pectoral arch with separate coracoid, precoracoid and interclavicle. Scapula without prespinous portion of blade. Pelvis with marsupial bones. Jaw extended, edentulous or with vestigial teeth. Oviparous. Mammary glands without nipples, opening into separate glandular areas. Urethra and genital passages opening into the cloaca, which leads into the lower extremity of the rectum. Body-temperature not similar everywhere.

This order is of interest on account of its many reptilian features and also because of its high degree of specialisation. It is, however, of little importance in

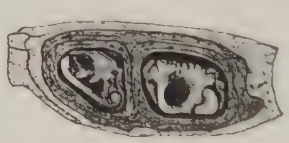


FIG. 25.
Lower left molars of the young of *Ornithorhynchus*. 5/2. (After O. Thomas.)

palaeontology, for the few definitely known remains are found in the Pleistocene of Australia and belong to the three recent genera, *Ornithorhynchus* (Fig. 25), *Echidna* (*Tachyglossus*) and *Proechidna*.

[1] *Gregory, W. K.*, The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. xxvii., 1909, pp. 144-162. – *Thomas, O.*, Dentition of *Ornithorhynchus*. Proc. Roy. Soc. Lond., vol. xlvi., 1889. —*Van Bemmelen, J. F.*, Der Schädelbau der Monotremen. (In Semon, Zoologische Forschungsreisen in Australien. Jena, 1901.)

Order II. MARSUPIALIA.[1]

(*Didelphia* Blainville; *Metatheria* Huxley.)

Herbivorous and carnivorous animals of highly diversified heterodont dentition. Pectoral arch with reduced coracoid and without precoracoid, pelvis with marsupial bones. Nipples usually enclosed in a skin fold, which forms a sack in which the young, incompletely developed at birth, are carried for a considerable period.

The marsupials constitute a large division of *Mammalia*, comprising carnivorous and insectivorous types as well as hoofed and rodent-like forms. These manifold variations are displayed not only in the dental but also in the skeletal structure. The brain is small, and the olfactory and optic lobes and the cerebellum are not covered by the smooth hemispheres of the cerebrum. The nasals are large, the jugal arch complete, and the orbits are open posteriorly. The alisphenoid takes part in the formation of the auditory capsule, less commonly the mastoid and semicircular tympanic. The hard palate is always perforated with larger or smaller foramina. The posterior angle of the lower jaw is inflected.

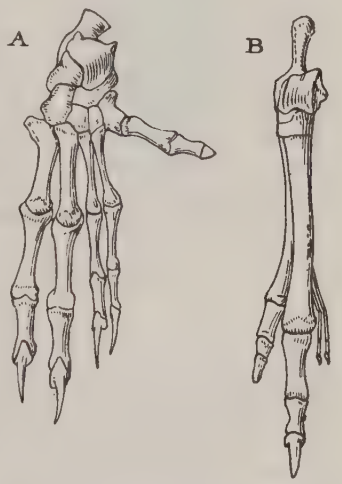


FIG. 26.

A, *Trichosurus*, hind foot with five subequal toes. *B*, *Macropus*, I.-III. toes reduced. (After Dollo.)

The teeth resemble in some respects those of herbivores and rodents, and in others insectivores and carnivores. Among the former the number of *I*, *P* and *C* teeth are greatly reduced, but to counterbalance this deficiency one of the *I* is very strongly developed in both jaws. The latter type has a complete set of teeth in which there are, as a rule, as many as $\frac{5}{4}$ *I* teeth. The *C* are very powerful, often having two roots. Also, the *P* are of very simple structure and medium size, only the most posterior one being large and often highly specialised. The majority of *M*, found in groups of four, are either secodont, bunodont or lophodont. Dental succession is limited to the last *P*. The jaw in the embryos of existing Marsupials contains the rudiments of more teeth than occur in the adult.

[1] *Ameghino, F.*, Los Diprotodontes del orden de los Plagiaulacoideos. Anal. Museo Nacion. Buenos Aires, vol. ix., 1903.—*Cope, E. D.*, The Tertiary Marsupialia. Amer. Naturalist, 1884.—*Goodrich, E. S.*, Mammalia from the Stonesfield Slate. Quart. Journ. Micros. Sci., vol. xxxv.—*Gregory, W. K.*, The orders of mammals. Bull. Amer. Mus. Nat. Hist., vol. xxvii., 1909, p. 162-231.—*Marsh, O. C.*, Amer. Journ. Sci., 1880, vol. xx.; 1881, vol. xxi.; 1889, vol. xxxviii.; 1892, vol. xliii.—*Osborn, H. F.*, Proc. Acad. Nat. Sci. Philad., 1887-88.—Journ. Acad. Nat. Sci. Philad., vol. ix., 1888.—Evolution of the mammalian molar teeth. New York, 1907.—*Owen, R.*, Monograph of fossil Mammalia of the British Mesozoic formations. Palaeontogr. Soc., 1871.—Researches on the fossil remains of the extinct mammals of Australia with a notice of the extinct marsupials of England. London, 1877.—*Sinclair, W. J.*, Marsupialia of the Santa Cruz beds. Rept. Princeton Univers. Exped. to Patagonia, vol. iv. part iii., 1906.—*Thomas, O.*, On the homologies and succession of the teeth in the Dasyuridae. Phil. Trans. Roy. Soc., 1887, vol. 178 *B*.—*Broom, R.*, Bull. Amer. Mus. Nat. Hist., 1914, vol. xxxiii. pp. 115-34.—*Matthew, W. D., ibid.*, 1916, vol. xxxv. pp. 477-500.—*Wood, H. E.*, Sparassodonts. Bull. Amer. Mus. Nat. Hist., 1924, vol. li. p. 77.—*Woodward, A. S.*, Diprotodon, Geol. Mag., 1907, p. 337.—Wealden Teeth, Q. Journ. Geol. Soc., 1911, p. 278.—Triconodon, Proc. Geol. Assoc., 1912, vol. xxiii. p. 100.

The marsupial bones, paired rod-like ossifications attached to the foremost extremity of the os pubis, are a peculiarly distinctive feature of the group. They are found in both sexes, but in the genus *Thylacinus* are represented only by a small, unossified fibro-cartilage. Frequently the length of the hind-limbs exceeds that of the anterior pair. The pes (Fig. 26) has either five or four toes, of which the fourth is the largest. The second and third among herbivorous marsupials become very slender, and are enclosed nearly to their extremities in a common integument. There exist, nevertheless, many transitions between this highly specialised form and the original five-toed foot. The hallux is often at right angles to the rest of the toes, in some cases even being eliminated entirely. Dollo traces the development of all marsupials from pentadactyl arboreal ancestors.

With the exception of the *Didelphiidae*, extensively found in America, and the South American *Caenolestidae*, the habitat of marsupials is at present restricted to Australia and the neighbouring islands. The Pleistocene forms of this order were similarly distributed. In the Jurassic, Cretaceous and Tertiary, however, fossil marsupials are found not only in America, but also, to a great extent, in Europe. Marsupials may be divided for purposes of practical convenience into three suborders, as follows: *Allotheria*, *Diprotodontia* and *Polyprotodontia*. The family *Caenolestidae* may be considered transitional between the last two.

Suborder A. ALLOTHERIA Marsh.

(*Multituberculata* Cope.[1])

Small extinct herbivorous or omnivorous mammals with polybunous M, the tubercles of which are arranged in two or three longitudinal series. P similar to M but simpler or laterally compressed. Each jaw with one strongly developed rodent-like I. No C. Lower jaw usually with inflected angle. Coracoid perhaps separately developed.

Remains of *Allotheria* have been found in the Trias of Europe and South Africa, in the Jura of Europe and North America, in the Cretaceous of North America and in the basal Tertiary of Europe and North America. Probably here should be placed also several forms from the Eocene of South America.

Most of the genera are represented by isolated teeth, mandibles, and more rarely portions of the upper jaw and cranium. The complete skull and various bones are known only in the genus *Ptilodus*. The systematic position of many forms is therefore very uncertain. Nevertheless the greater number of forms may be regarded as marsupial. It has been shown by Matthew that Cope was in error in referring an astragalus to *Polymastodon*.

Family 1. Tritylodontidae Cope.

Snout truncated, premaxillary with one stout canine-like I, followed by a small pointed I. P similar to M, but simpler: M with three rows of tubercles. Trias; South Africa and Europe.

[1] *Ameghino, F.*, Anales Mus. Nac. Buenos Aires, vol. ix., 1904. — *Cope, E. D.*, Amer. Naturalist, 1881, vol. lxxxvi. — *Broom, R.*, Bull. Amer. Mus. Nat. Hist., vol. xxxiii., 1914. — *Gidley, J. W.*, Proc. U.S. Nat. Mus., vol. xxxvi., 1909, p. 611. — *Hennig, E.*, Neues Jahrb. f. Min., Beil.-Bd. 46, 1922. — *Lemoine, V.*, Bull. Soc. Géol. France, 1883, 3 sér. — *Marsh, O. C.*, Amer. Journ. Sci., 1878–81; 1889; 1892. — *Osborn, H. F.*, Journ. Acad. Nat. Sci. Philad., vol. ix., 1888. — Proc. Acad. Nat. Sci. Philad., 1891. Amer. Naturalist, July 1891. — Bull. Amer. Mus. Nat. Hist., 1893.

Tritylodon Owen (Fig. 27). According to Broom, this genus belongs to the *Allotheria* (*Multituberculata*). Karoo formation of South Africa.

Fig. 27.

Tritylodon longaevus Owen. Triassic of Basutoland. Skull from above and below. 2/3. (After Owen.)

Triglyphus Fraas. Known only by minute quadrangular teeth with two or three rows of tubercles. Rhaetic Bonebed of Hohenheim near Stuttgart.

Family 2. **Plagiaulacidae** Gill.

Premaxillary with one to three I, mandible with one I. First I, in both jaws rodent-like. Upper P with three to five tubercles, the hindermost frequently with more. Lower P laterally compressed, trenchant with jagged edges. Lower M with two, upper with three rows of tubercles; rarely only two rows present in upper M. Lower jaw less elongated than the upper. The articular condyle extends as far as the inflected angle. Rhaetic; Europe. Jurassic to Eocene; Europe and North America.

Microlestes Plieninger (*Hypsiprymnopsis* Dawkins)

Fig. 28.

Microlestes antiquus Plieninger. Molar from the Bonebed of Echterdingen, Württemberg. 3/1.

Fig. 29.

Plagiaulax becklesi Falc. Purbeck beds of Swanage, Dorsetshire. *A*, Lower jaw, 1/1. *B*, *Plagiaulax minor* Owen, from the same locality. *a*, molar enlarged; *b*, lower jaw enlarged; *c*, the same, 1/1. (After Falconer.)

(Fig. 28). Known only by small, elongated quadrangular teeth, excavated in the middle and with tubercles along the inner and outer margins. Rhaetic Bonebed of Württemberg and Somersetshire.

Plagiaulax Falconer (*Bolodon* Owen) (Figs. 29, 30). $\frac{2.0.3.4.}{1.0.3\text{-}4.2}$. Mandible

with high coronoid process and low articular condyle extending beyond the angle of the jaw. Anterior upper *I* directed vertically downward, and lower first *I* directed obliquely upward and forward. Upper *P* with biserially arranged rows of tubercles, and lower *P* increasing in size in a posterior direction, trenchant, lamellar, and with channelled lateral surfaces. Upper and lower *M* each with two rows of tubercles. Purbeck and Wealden; England.

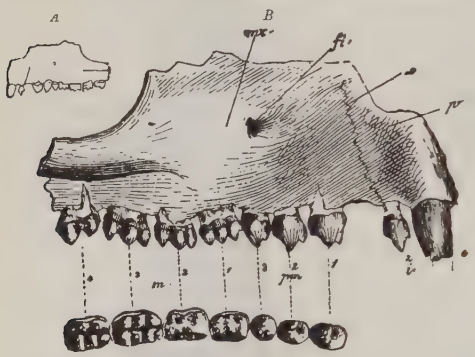


Fig. 30.

Bolodon crassidens Owen. Purbeck beds of Dorsetshire. *A*, Fragment of upper jaw, $^1/_1$. *B*, The same, $^4/_3$ (after Osborn). *mx*, maxilla; *pmx*, premaxilla; *s*, suture between maxilla and premaxilla; *fi*, infraorbital foramen; *i*, incisors; *pm*, premolars; *m*, molars.

Allodon Marsh. Upper jaw similar to that of *Plagiaulax*, but with three *I*. Upper Jura; Wyoming.

Fig. 31.

Allacodon pumilus Marsh. Upper Cretaceous of Wyoming. *a*, the three premolars of the upper jaw, $^1/_1$; *b*, the same, $^3/_1$. (After Marsh.)

Allacodon Marsh (Fig. 31). Upper Cretaceous; North America.

Ctenacodon Marsh (Fig. 32). Lower *P* slightly channelled on the upper surface. Upper *M* with only two large tubercles on the outer face. Upper Jura; Wyoming.

Neoplagiaulax Lemoine (*Liotomus* Cope). Lower jaw with only one large grooved *P* and two *M*. Lower Eocene of Rheims, France, and New Mexico, U.S.A.

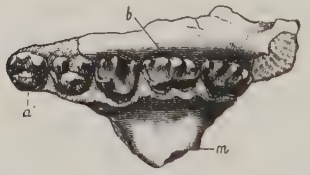


Fig. 32.

Ctenacodon potens Marsh. Upper Jurassic of Wyoming. Lower aspect of right upper jaw, $^4/_1$ (after Marsh). *a'*, first premolar, and *b*, fourth premolar; *m*, maxillary base of zygomatic arch.

Fig. 34.

Cimolomys (*Cimolodon*) *nitidus* Marsh. Upper Cretaceous of Wyoming. (After Marsh.) *a*, Next to the last molar of the lower jaw, $^1/_1$; *b*, the same enlarged.

Fig. 33.

Ptilodus gracilis Gidley. Lowest Eocene of Fort Union beds, Montana. *A*, Skull and lower jaw. *B*, Upper jaw. *C*, Lower jaw. $^2/_3$. (After Gidley.)

Ptilodus Cope (*Chirox* Cope) (Fig. 33). $\frac{1.1.4.2.}{1.0.2.2.}$. Skull depressed and flat with a long, broad snout, palate with large foramen, and articular condyle situated near the broadly expanded occiput. Upper *C* resembling *I* but smaller, P^1 with three, P^2 with four, P^3 with six tubercles, and P^4 elongated, with numerous tubercles. M^1 narrower than P^4. P_3 reduced, P_4 strongly developed, and grooved on both sides. M_1 with more numerous tubercles than M_2. Humerus massive, with small entepicondylar foramen. The pelvis, femora, and lower limb-bones are also known. Lowest Eocene; Montana and New Mexico.

Cimolomys Marsh (*Cimolodon*, *Nanomys* Marsh, *Ptilodus*, *Halodon* Osborn) (Fig. 34). Upper *M* with three rows of tubercles. Upper Cretaceous (Laramie); Wyoming and Montana. Middle Cretaceous of North-West Canada.

Meniscoëssus Cope (*Dipriodon*, *Tripriodon*, *Selenacodon*, *Oracodon* Marsh) (Fig. 35). Isolated teeth are practically the only known remains. Upper *M* with three rows of tubercles. Upper Cretaceous (Laramie); North America. Wealden; England.

Family 3. **Polymastodontidae** Cope.

Both jaws with a strong, rodent-like I on each side and two large M, in front of which is a small, simple P, separated from the I by a long diastema. The large upper I followed by a small I. The lower M have two, the upper three longitudinal series of stout tubercles. Angle of lower jaw inflected. Articular condyle lying almost in the occipital plane. Basal Tertiary (Puerco); New Mexico.

Polymastodon Cope (*Taeniolabis*, *Catopsalis* Cope) (Fig. 36). $\frac{2.0.1.2.}{1.0.1.2.}$. Attaining about the size of a beaver.

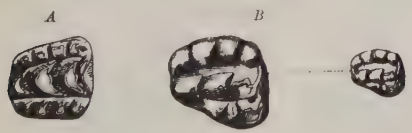


Fig. 35.

A, *Meniscoëssus conquistus* Cope. Upper molar from the Upper Cretaceous (Laramie formation) of Dakota; $^2/_1$ (after Osborn). *B*, *Tripriodon coelatus* Marsh. Upper Cretaceous of Wyoming. Probably the last upper molar. $^1/_1$ and $^2/_1$ (after Marsh).

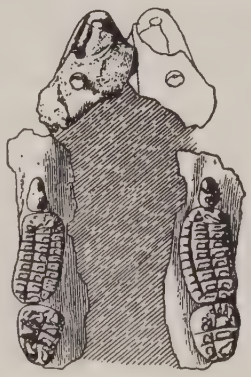


Fig. 36.

Polymastodon attenuatus Cope. Lowest Eocene of New Mexico. Palate with both tooth rows. $^1/_1$. (After Osborn.)

Family 4. **Polydolopidae** Ameghino.

Lower I almost horizontal. P^3, P^4 and lower P_4 higher than M and most frequently developed to form a cutting surface. Upper M with two or three series of tubercles, lower always with two only and diminishing in size posteriorly. Three, less often five tubercles in a row. $\frac{1.0.2.3.}{1.0.1\text{-}2.3.}$. Early Tertiary; Patagonia.

These are possibly the descendants of *Plagiaulacidae*. Their relationship with the *Caenolestidae* is rather doubtful on account of their large size, although there are certain resemblances between *Polydolops* and *Abderites*.

The family is represented by numerous genera established by Ameghino mostly upon detached teeth. *Orthodolops* and *Amphidolops* have the tubercles

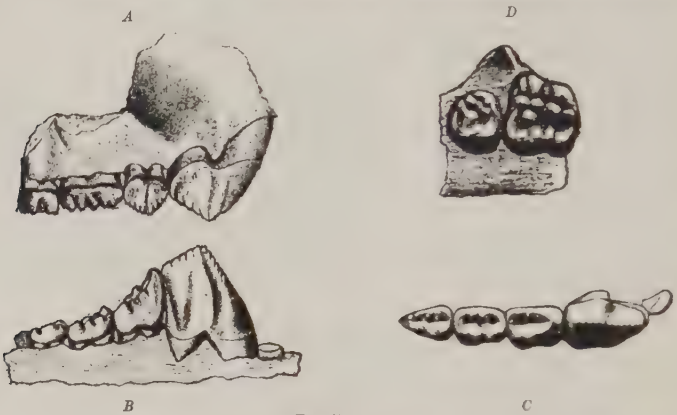


FIG. 37.

Polydolops thomasi Ameghino. Notostylops strata of Eocene; Patagonia. *A*, Upper tooth row. *B*, External aspect of lower tooth row. *C*, *B* from above. *D*, *Pliodolops primulus* Ameghino. Same locality. Upper M. $^4/_1$. (After Ameghino.)

but slightly differentiated, and *Polydolops* (Fig. 37, *A-C*), *Pseudolops* and *Pliodolops* have them well defined. *Pliodolops* (Fig. 37, *D*) has the tubercles of the upper molars arranged in several series.

Propolymastodon (*Promysops* ?) Ameghino (Fig. 38) $\frac{1.0.2.3.}{1.0.1.3.}$ is distinguished from the other genera in possessing only one very simple, non-corrugated lower *P.*

Eommanodon Ameghino. Miocene (Colpodon beds). Systematic position doubtful.

FIG. 38.

A, *Propolymastodon caroli ameghinoi* Ameghino. Lower jaw. $^2/_3$. *B*, *P. acuminatus* Ameghino. Left last lower M, $^2/_1$. *C*, *P. cardatus* Ameghino. Lower tooth row with exception of last M., seen from above, $^1/_1$. Notostylops strata of Upper Eocene; Patagonia.

Suborder B.

DIPROTODONTIA Owen.

Chiefly herbivorous forms with four quadritubercular or two ridged M. P similar to M or laterally compressed (lamellar ?) and trenchant. C lacking or very minute. Above, 4-1 I, of which the foremost is enlarged; below, only a single, very strong, rodent-like I.

The *Diprotodontia* are possibly descendants of *Polyprotodontia*, which have adapted themselves to a mixed or exclusively herbivorous diet. With the exception of the South American genus *Caenolestes* they are confined to Australia, where they also exist in the Pleistocene. From the Tertiary of Patagonia a number of extinct genera and species are known.

Family 1. Caenolestidae Trouessart.

(*Paucituberculata* Ameghino.)

Small or moderate-sized marsupials with three to four small vertical upper I and a large, lower I, horizontally placed. Behind are three to four simple, pointed teeth, of which one in the upper jaw often becomes a strong C. Upper P^2 *and* P^3 *small,* P^4 *larger and with cutting edge, as are also the two lower P. M quadricuspidate, decreasing in size backwards. Lower* M_1 *frequently enlarged, with five cusps and functioning, together with* P^4*, as a pair of scissors. The remaining M are quadritubercular and lophodont. Upper M with weak, secondary inner cusp. Feet not syndactylous.* Recent and fossil in South America.

Subfamily 1. Caenolestinae.

$\frac{4.1.3.4.}{1.0.4\text{-}5.4.}$ *No P or M developed as cutting teeth. Lower M is a tuberculosectorial tooth. P and M very like those of Didelphys.*

Caenolestes Thomas. Living in Ecuador.

Garzonia (Fig. 39, *A*) and *Halmarhiphus* Ameghino from the Miocene of Santa Cruz; the former genus with tritubercular upper *M*.

Stilotherium (Fig. 39 *B*) and *Cladoclinus* Ameghino (*Pitheculites, Clenialites* Ameghino). Miocene of Patagonia.

Zygolestes Ameghino. Pliocene. Parana beds of Argentina.

Fig. 39.

A, Garzonia typica Ameghino. Miocene of Santa Cruz. Upper M., inferior and rear aspect, 3/2. *B, Stilotherium dissimile* Ameghino. Same locality. Lower jaw, 1/1. (After Ameghino.)

Subfamily 2. Palaeothentinae.

$\frac{?\,1.3.4.}{1.0.4\text{-}3.4.}$ *Upper* P^4 *and lower* M_1 *together form scissors. In the lower jaw behind I are three to four small intermediate teeth. Skull, more especially the occiput, is very broad. Zygomatic arch very prominent.*

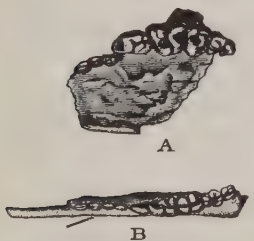


Fig. 40.

A, Palaeothentes intermedius Ameghino. Upper molars. *B, P. minutus* Am. Lower molars. Upper Miocene of Santa Cruz. 3/2. (After Sinclair.)

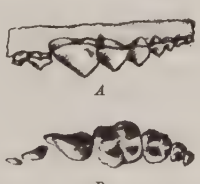


Fig. 41.

Metaepanorthus holmbergi Ameghino. *A*, Exterior aspect of upper tooth row. *B*, Inferior aspect of same, 2/1. Upper Miocene of Santa Cruz, Patagonia.

Palaeothentes Moreno (Fig. 40). *Epanorthus, Metaepanorthus* (Fig. 41),

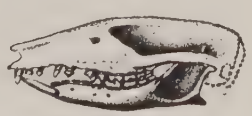


Fig. 42.

Paraepanorthus minutus Ameghino. Exterior aspect of skull and lower jaw. 1/1. Upper Miocene of Santa Cruz, Patagonia.

Paraepanorthus (Fig. 42) Ameghino. All *M* nearly uniform in size. *P* robust. *Callomenus* (Fig. 43), *Decastis, Acdestis* Ameghino. Miocene of Patagonia. *M* of

greatly varying size. *Dipilus, Metriodromus, Halmaselus, Pichipilus, Essoprion* Ameghino are imperfectly known. *Palaepanorthus* Ameghino. Lower Miocene (Pyrotherian beds).

Subfamily 3. ABDERITINAE.

$\frac{? \; ? \; ? \; ?}{1.0.4\text{-}5.4.}$ *P^4 enlarged, lower M_1 developed as cutting tooth with grooves on either side; the remaining M are bunolophodont and quadritubercular.*

The lower M_1 has a marked resemblance to P_4 of *Allotheria*, but possesses a heel which is but weakly developed in the forms from the Colpodon beds. Miocene of Patagonia.

Abderites Ameghino (Fig. 44). Between I_1 and the small transversely placed P_4 are four intermediate teeth. Miocene; Santa Cruz.

Parabderites Ameghino. Between I_1 and the rather large P_4 are five intermediate teeth. Colpodon and Pyrotherian beds (Miocene).

FIG. 43.

Callomenus robustus Ameghino. Inner aspect of lower jaw. 1/1. Upper Miocene of Santa Cruz, Patagonia.

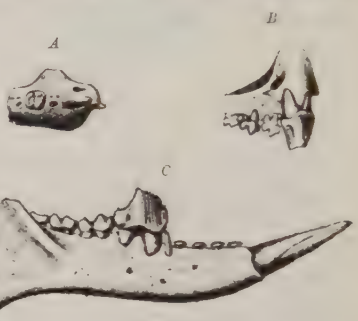


FIG. 44.

Abderites meridionalis Ameghino. *A*, Inferior aspect of upper jaw, 1/1. *B*, Exterior aspect of same, 1/1. *C*, Exterior aspect of lower jaw, 3/2. Upper Miocene of Santa Cruz, Patagonia.

Family 2. **Phalangeridae.**

Diversely specialised marsupials, some omnivorous, some herbivorous, adapted partly for leaping, partly for climbing, and even sometimes for flying. Dentition never complete. $\frac{3.1.3\text{-}1.4.}{1.0.3\text{-}1.4.}$ *Upper I^1 larger than the rest, lower I horizontal and rodent-like. Upper C always small; P_4 in both jaws almost always trenchant, usually grooved, or else all P are M-like. M quadricuspidate, tubercles of uniform size and united in pairs. Fore limbs generally shorter than hind; the fourth digit is always the most strongly developed. Second and third digits reduced and enveloped in a single fold of skin. Tail mostly long and powerful, and used partly as prehensile organ, partly for diminishing speed.*

Recent in Australia and in parts of New Guinea. Fossil in the Pleistocene of Australia.

Subfamily 1. HYPSIPRYMNINAE. Kangaroo-rats.

Long-snouted marsupials, not larger than a rabbit. $\frac{3.1.1.4.}{1.0.1\text{-}2.4.}$ *P_4 in both jaws, trenchant and channelled on both sides. Limbs of equal length. Pes usually pentadactyl.*

Aepyprymnus and *Bettongia* (Fig. 45), the latter without hallux. Recent in Australia, fossil in the Pleistocene of New South Wales. *Hypsiprymnodon* Rams. With two *P*.

Wynyardia Baldwin Spencer. Tertiary (Turritella Sandstone of Table Cape). Having the characteristics of *Diprotodontia* and *Polyprotodontia* combined in the form of skull and limbs. Systematic position uncertain on account of want of information regarding the dentition.

FIG. 45.
Bettongia grayi Gould. Skull. Recent. Australia.

Subfamily 2. THYLACOLEONINAE Owen.

$\frac{3.1.3.1.}{1.0.2.3.}$ *Large extinct marsupials with powerful pair of* I_1 *and long, trenchant* P_4. *The intermediate teeth and M very much reduced.*

Thylacoleo Owen (Fig. 46). Skull approximating to that of lion in size, occiput broad, snout very much foreshortened and narrowed. Zygomatic arch very robust and prominent. Skeleton not completely known. Terminal phalanges of the pes modified as large, strong, bent claws. In the Pleistocene of Australia, especially in bone caverns.

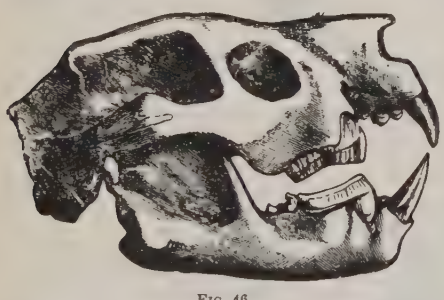


FIG. 46.
Thylacoleo carnifex Owen. Lateral aspect of skull. 1/5. Pleistocene of Queensland. (After Owen.) The post-orbital bar is wrongly shown as complete.

Subfamily 3. PHALANGERINAE.
Climbing and Flying Marsupials.

$\frac{3.1.3\text{-}2.4.}{1.0.2\text{-}1.4.}$ *Fore- and hind-limbs pentadactyl; the second and third digits of the latter are slender and fused together.*

Several of the genera living in Australia are also represented in the Pleistocene.

Subfamily 4. MACROPODINAE. Kangaroos.

$\frac{3.0\text{-}1.2\text{-}1.4.}{1.0.2\text{-}1.4.}$ *Upper I chisel-shaped, lower rodent-like and horizontal. P and M with large transverse ridges. Hind-limbs very much elongated, fifth, second and third toes reduced and the two latter covered by a single fold of skin. Hallux rudimentary.*

Besides the recent genus *Macropus* Shaw (*Halmaturus* Illiger), in Australia, there are found in the Pleistocene of that continent a number of fossil forms (*Sthenurus, Palorchestes* Owen, etc.) of large size.

Family 3. Phascolomyidae. Wombats.

Compact, rodent-like herbivorous marsupials with large head, short neck, short legs and stumpy tail. $\frac{3\text{-}1.0.1.4.}{1.0.1.4.}$. *I elongated above and below. Molars brachyodont or prismatic. Extremities clumsy, five-toed, fore- and hind-limbs nearly of equal length.* Recent and Pleistocene of Australia.

FIG. 47.

Diprotodon australis Owen. Lateral aspect of skull and lower jaw. Greatly reduced.

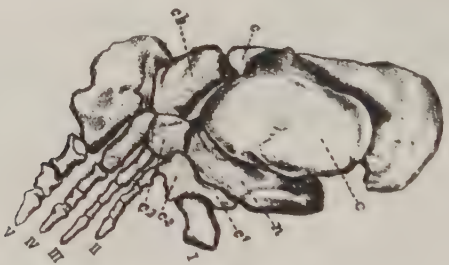


FIG. 48.

Diprotodon australis Owen. Pleistocene of Lake Kallabonna, S. Australia. Right hind-foot, greatly reduced. (After Stirling and Zietz.)

Phascolarctus Blainv. $\frac{3}{1}$ *I.* Molars brachyodont with four V-shaped tubercles which may sometimes become more numerous and conical in form.

Phascolomys Geoffroy. $\frac{1}{1}$ *I.* Molars cylindrical, consisting of two transverse ridges, each of which is composed of two V-shaped tubercles.

Phascolonus Owen. Fossil in the Pleistocene, distinguished on account of its very great size.

Nototherium and *Diprotodon* Owen (Figs. 47, 48). $\frac{2}{1}$ *I.* Extinct genera first found in the Pleistocene of Queensland and New South Wales, the typical

species about as large as rhinoceroses. Of *Nototherium* a nearly complete skeleton has been found in Tasmania. Of *Diprotodon* several skeletons from Lake Kallabonna, S. Australia, are known. All the phalanges of the first digit of the hind-foot are fused into a single piece. Manus and pes practically consist only of the enlarged carpals and tarsals and the fifth metapodium. *P* and *M* are formed by two transverse ridges separated by a broad valley.

Suborder C. POLYPROTODONTIA Owen.

Carnivorous or insectivorous marsupials mostly of small or moderate size. Dentition complete. In the upper jaw 4-5, *seldom* 3; *in the lower jaw* 3-4 *small I. C pointed and high, frequently with two roots; P with single cusps, less frequently with secondary cusps, and mostly with double root; M in the fossil forms often in greater number, in the recent forms four, triconodont and tritubercular.*

To the polyprotodont marsupials belong the Australian *Myrmecobiidae*, *Peramelidae*, *Notoryctidae*, *Dasyuridae*, the American *Didelphyidae*, and a large number of fossil forms, among which the Pleistocene and Tertiary are closely related to living genera, whereas the Mesozoic forms show peculiar, primitive characteristics which make their classification in the zoological system difficult. Owen considered the latter to be ancestors of the *Polyprotodontia*, and yet emphasised their relationship to placental insectivores.

Family 1. Dromatheriidae Osborn.

(*Protodonta* Osborn ? *Promammalia* Haeckel.)

P styliform with a single point. M with large central cone and smaller cusp in front and behind, root imperfectly divided. Lower jaw consists principally of the dentary bone; may have slight angular process.

These small forms, represented by few imperfect remains, acquire special significance, because they are thought to furnish a connecting link between the *Cynodontia* and mammals.

Dromatherium Emmons (Fig. 49). 3.1.4.6. Lower *I* upright, foremost *P* inclined forward, mandible without angular process. *Microconodon* Osborn. With lower *M* and slight angular process, perhaps with a separate angular bone in the mandible. Upper Trias of North Carolina.

Fig. 49.

Dromatherium sylvestre Emmons. Upper Triassic of Chatham, North Carolina. Lower jaw. 1/1.

Tribolodon Seeley. *M* with strong secondary cusps, but imperfectly divided root, without angular process. *Karoomys* Broom, from the Trias of South Africa, is imperfectly known.

Family 2. Triconodontidae Osborn.

Small marsupials with 4 *P and* 3-6 *M. Roots of the M absolutely divided. P similar to M but simpler. M with three cusps arranged in a single row and a conspicuous basal ridge or cingulum. C frequently with two roots. Angle*

of the lower jaw inflected. Condyle not sharply distinguished from the angle. Coronoid process broad. Dental succession restricted to last P. Jura of England and North America.

Triconodon Owen (*Triacanthodon* Owen) (Fig. 50). $\frac{?\,1.4.3\text{-}4.}{3.1.4.3\text{-}4.}$. Upper *C* with two roots. *P* with small fore and hind cusp, *M* with three cusps of almost the same size. Purbeck beds of England.

Priacodon Marsh. Upper Jura of Wyoming.

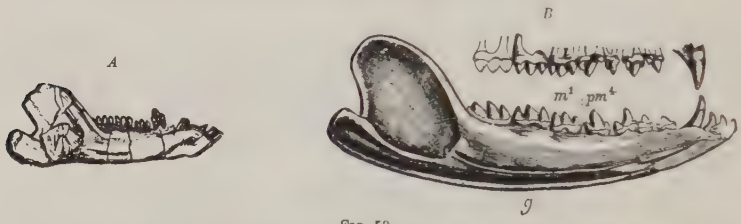


FIG. 50.

Triconodon mordax Owen. Purbeck strata of Durdlestone Bay, Dorset. *A*, Lower jaw, $^1/_1$ (after Owen). *B*, Upper jaw dentition and lower jaw, $^2/_1$. Restoration. (After Osborn.)

Amphilestes Owen. $\frac{\quad}{4.1.4.5.}$. *P* and *M* differing but slightly. Middle cusp higher than those in front and behind. Great Oolite; Stonesfield, England.

Phascolotherium Owen. $\frac{\quad}{4.1.3.5.}$. Behind the *C* a diastema. Central cusp of *P* and *M* higher than side-cusps. Great Oolite; Stonesfield, England.

Menacodon Marsh. $\frac{\quad}{?\,1.3.4.}$. Secondary cusps smaller than primary cusp and slightly inflected. Upper Jura; Wyoming.

Tinodon Marsh. Upper Jura; Wyoming.

Spalacotherium Owen. $\frac{\quad}{3.1.4.6.}$. Purbeck; England. *S. tricuspidens* Owen.

Family 3. **Pantotheriidae** (*Trituberculata* Osborn, *Pantotheria* Marsh).

Small insectivores, having the lower jaw without inflected angle, with primitive, tuberculo-sectorial lower M and tritubercular upper M. Lower I usually forwardly inclined, P_3 and P_4 larger than M. Generally eleven teeth, 4 P, 7 M, following the canine. Jura and Upper Cretaceous of England and North America.

These small forms, restricted to the late Mesozoic, are referred to the *Placentalia* by Osborn. Nevertheless it cannot be denied that certain of these represent the ancestral forms from which the *Insectivora* and *Creodontia* are descended. At the same time they are related to *Triconodontidae*, and also to *Myrmecobius*. The latter form is clearly marsupial, notwithstanding the slightly inflected angle of the lower jaw. The large number of *M* is sufficient reason for placing it among the latter forms. The trigonid of the lower *M*, arising from the protoconid, paraconid and the metaconid, is well developed; the talonid, however, is still very small and is represented only by a single

tubercle. The *M* also sometimes have but one point, owing to reduction. The three tubercles of the upper *M* often develop secondary tubercles.

Subfamily 1. AMPHITHERIINAE Owen.

Lower I's almost vertical, lower M's tuberculo-sectorial with strong, two-rooted talonid. Coronoid process broad, angle of the mandible rounded, downwardly directed. Articulation situated low down. Behind C there are nine to twelve teeth.

Amphitherium Blainville (*Thylacotherium* Val.) (Fig. 51). Middle Jura of England. $\frac{\_\_\_\_}{4.1.5.6.}$. A jaw found in 1818 was assigned to marsupials by Cuvier, and to reptiles by Blainville.

Amphitylus Osborn. Same horizon and locality.

Peramus, Leptocladus Owen. Upper Jura (Purbeck); England.

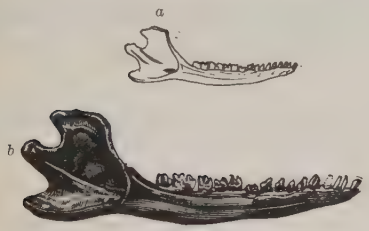


FIG. 51.

Amphitherium prevosti Blv. Great Oolite; Stonesfield, near Oxford. Exterior aspect of left half of lower jaw. *a*, 1/1; *b*, 2/1. (After Owen.)

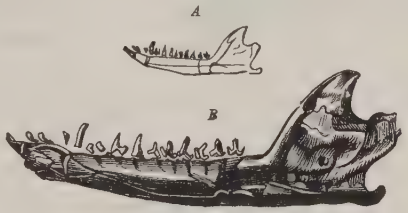


FIG. 52.

Amblotherium soricinum Owen. Upper Jurassic of Purbeck, England. Right half of lower jaw. *A*, 1/1. *B*, 3/1. (After Owen.)

Subfamily 2. AMBLOTHERIINAE Osborn (*Stylacodontidae* Marsh).

M gradually becoming a single cone, single-rooted. C with a single root, coronoid process slender, angle of lower jaw not sharply accentuated. I forwardly inclined, P_3 and P_4 larger than M. Behind C eleven to twelve teeth.

Amblotherium Owen (Fig. 52). Upper Jura (Purbeck); England. $\frac{\_\_\_\_}{4.1.4.6.}$. Probably the upper *M* of *Peralestes* Owen belong here, which have besides protocone, metacone and paracone also parastyle and metastyle.

Peraspalax Owen and *Achyrodon* Owen. Upper Jura (Purbeck); England.

Phascolestes (*Dryolestes*) Marsh. Upper Jura; Wyoming.

Laodon and *Asthenodon* Marsh. Same horizon and locality.

Stylodon Owen (*Stylacodon*? Marsh). Upper *M*. *Kurtodon* Osborn (Fig. 53). Upper Jura (Purbeck); England.

Subfamily 3. PAURODONTINAE Marsh.

M two-rooted, indistinctly tuberculo-sectorial, with minute secondary tubercles. Lower jaw short and massive. Not more than seven teeth following C. Jura of Wyoming.

Paurodon Marsh. Apparently $\frac{\_\_\_\_}{3.1.4.3.}$ like most Placentalia.

Subfamily 4. DIPLOCYNODONTINAE Marsh.

Upper M with large protocone, lower M with broad, basin-like talonid. Jura of Wyoming.

Dicrocynodon Marsh (*Diplocynodon* Marsh) (Fig. 54). $\frac{\quad}{3.1.4.8.}$. Median cone of *M* and *P* high. Coronoid process broad. Angle small. Articular condyle above the summits of teeth.

Enneodon, *Docodon* Marsh.

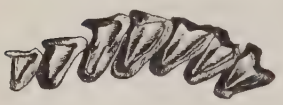


FIG. 53.

Kurtodon Osborn. Upper molars enlarged. Upper Jurassic of England. (After Osborn.)

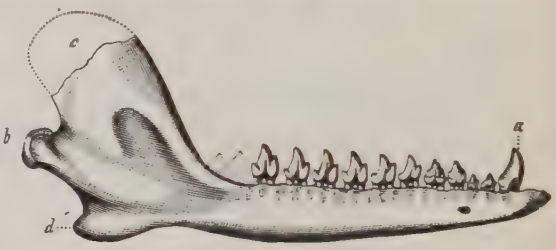


FIG. 54.

Dicrocynodon victor Marsh. Upper Jurassic of Wyoming. Exterior aspect of right half of lower jaw. $^2/_1$ (after Marsh). *a*, canine; *b*, condyle; *c*, coronoid process; *d*, angle.

Family 4. **Notoryctidae** Stirling.

Limbs specialised for digging as in moles.

Notoryctes Stirling. Recent in Australia.

Family 5. **Peramelidae.**

Limbs very much specialised. Hand often fitted for digging. Pes with reduced lateral toes. Recent in Australia. Represented in the Pleistocene of Australia by a few fragmentary remains.

Family 6. **Dasyuridae.** Predaceous Marsupials.

Carnivorous marsupials of moderate size. $\frac{3\text{-}4.1.3.4.}{3.1.3.4.}$. *I and C normally developed. Upper M tritubercular with two outer cusps, one large inner cusp, protocone, and one trenchant metastyle. M^4 usually very much reduced. Lower M with trenchant anterior cusp, paraconid, primary cusp, protoconid, and small hollowed or secodont talonid, but no metaconid. P in both jaws with single cusp, bifid root, gradually becoming larger antero-posteriorly, P_4 seldom enlarged. Manus with five clawed toes; pes with five or four toes, hallux frequently reduced, sometimes wanting. Angle of lower jaw inflected.*

In the case of the genera *Dasyurus* Geoffr., *Sarcophilus* Cuv. and *Thylacinus* Temm., Recent and also Pleistocene in Australia, only the hindmost of the three *P* is modified. The hard palate is perforated.

Among the following genera, found only in the Tertiary of Patagonia and constituting the *Sparassodonta* of Ameghino, the palatal perforation is lacking and *C* as well as two *P* succeeds a milk tooth.

Cladosictis Ameghino (Fig. 55). $\frac{4}{3}$ *I.* M^{1-3} with strong protocone. M^4 strongly reduced. Lower *M* with rather stout talonid. *P* gradually increasing in size. Skull with alisphenoid bulla. Hallux reduced.

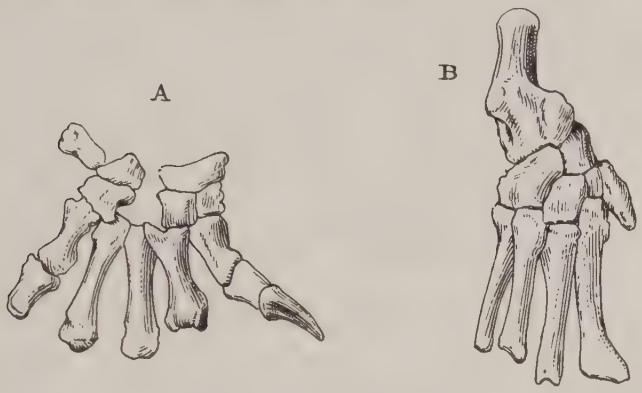


FIG. 55.

Cladosictis lustratus Ameghino. Upper Miocene of Santa Cruz, Patagonia. *A*, Hand. *B*, Foot. $\frac{1}{1}$. (After Sinclair.)

Humerus with entepicondylar foramen. Claws pointed, compressed. Miocene; Santa Cruz.

Hathlyacynus Mercerat. Same locality and horizon. *Procladosictis*, *Pseudocladosictis* Ameghino. Eocene. Notostylops beds.

Amphiproviverra (*Protoproviverra*) Ameghino (Fig. 56). $\frac{4}{3}$ *I.* Upper *M* with three strong cusps and short metastyle. M^4 slightly reduced. Lower *P* and *M* slender, *M* with large, hollowed-out talonid. Hallux large, opposable. Humerus without foramen. Claws pointed. Miocene; Santa Cruz.

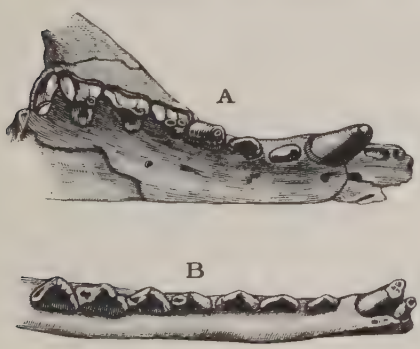


FIG. 56.

Amphiproviverra manzaniana Ameghino. Upper Miocene of Santa Cruz. *A*, Upper dentition. *B*, Lower dentition. $\frac{1}{1}$. (After Sinclair.)

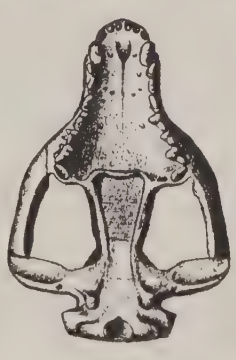


FIG. 57.

Borhyaena tuberculata Ameghino. Skull. $\frac{1}{5}$. Upper Miocene of Santa Cruz, Patagonia. (After Ameghino.)

Perathereutes, *Sipalocyon*, *Agustylus*, *Acyon*, *Ictioborus* Ameghino. Miocene; Santa Cruz.

Prothylacinus Ameghino. $\frac{4}{3}$ *I.* M^1 and M^2 with well-defined protocone, M^3 without, M^4 with small protocone and metacone, P^4 slightly larger than P^3. Lower *M* with small talonid. Skull long, without alisphenoid bulla. Lower jaw with firm symphysis. Hallux very much reduced. Claws pointed and compressed. Miocene; Santa Cruz.

Napodonictis Ameghino. Santa Cruz. *Pseudothylacinus* Ameghino. Miocene. Colpodon beds.

Borhyaena Ameghino (Fig. 57). $\frac{3}{3}$ *I.* Stocky teeth, closely set. M^4 button-like. Talonid well developed only on M_1 and M_2. Skull short with protruding zygomatic arch. Without alisphenoid bulla. Humerus without entepicondylar foramen. The terminal phalanges blunt, round and with furcate extremity. Miocene; Santa Cruz.

Acrocyon, Conodonictis Ameghino. Miocene; Santa Cruz. *Pseudoborhyaena* Ameghino. Miocene. Colpodon beds. *Proborhyaena, Pharsophorus* Ameghino. Pyrotherium beds.

Family 7. Didelphyidae. Opossums.

Generally small carnivorous marsupials. $\frac{5.1.3.4.}{4.1.3.4.}$ *I small, very closely set. C well-developed. Preceding the last, usually very high P, is a long functioning milk-tooth. Upper P tritubercular and triangular, protocone, paracone and metacone V-shaped, usually having a few small basal tubercles along outer edge. Lower M tuberculo-sectorial, with strong metaconid and multitubercular, well-developed talonid. Extremities five-toed, hallux opposable. Humerus with entepicondylar foramen.*

Both of the existing genera, *Didelphys* and *Chironectes*, are found in America ranging from Patagonia to Canada. Fossil representatives are not uncommon in the early Tertiary of Europe and North America, in South America in the Tertiary and Pleistocene. The oldest forms are known from the Laramie of North America. Of the genera *Didelphops, Cimolestes, Pediomys, Telacodon* and *Batodon* Marsh, from the Upper Cretaceous of Wyoming, only isolated teeth and fragmentary jaws are known.

Didelphys Linn. (*Peratherium* Aymard, *Oxygomphius* Meyer, *Amphiperatherium* Filhol, *Herpetotherium, Embassis* Cope) (Fig. 58). $\frac{5.1.3.4.}{4.1.3.4.}$ Besides the three principal V-shaped tubercles there exist also on the outer edge of the upper *M* secondary tubercles. Lower *M* slender. In Europe from the Upper Eocene to the Lower Miocene, in North America in the Eocene, Oligocene and Pleistocene.

Fig. 58.

Didelphys (Oxygomphius) frequens H. v. Meyer. Miocene of Eckingen, near Ulm. *a, b, c*, three teeth from upper jaw, $^3/_1$; *d*, lower jaw, $^1/_1$; *e*, same enlarged. (After Schlosser.)

Microbiotherium Ameghino. *I* strong. Upper *M* consisting of three conical tubercles and a simple basal ridge, lower massive with large talonid. Upper Miocene; Santa Cruz. There also the problematic genera *Hadrorhynchus, Stylognathus, Eodidelphys* Ameghino. In the Eocene, Notostylops beds of Patagonia, *Ideodidelphys* Ameghino. *Proteodidelphys* Ameghino, supposedly from Cretaceous strata of Patagonia.

Family 8. Caroloameghiniidae Ameghino.

$\frac{5.1.3.4.}{4.1.3.4.}$. *C small, P simple and elongated. Upper M tritubercular with intermediate tubercles. Lower M with low trigonid and large talonid and secondary tubercles before and behind the high metaconid. Lower jaw slender and low.*

The *M* resemble in form partly those of *Primates*, partly those of *Rodentia*.

Caroloameghinia Ameghino (Fig. 59). Eocene. Notostylops beds of Patagonia.

FIG. 59.

Caroloameghinia mater Ameghino. Upper Eocene; Notostylops beds, Patagonia. *a*, inferior aspect of upper molar; *b*, superior aspect of M_1 and M_2, $^3/_1$; *c*, lower jaw, $^1/_1$. (After Ameghino.)

GEOLOGICAL AND GEOGRAPHICAL DISTRIBUTION OF MARSUPIALS.

	Trias.			Middle Jurassic.	Upper Jurassic.		Upper Cretaceous.	Tertiary.				Pleistocene.		Recent.	
	Europe.	North America.	South Africa.	Europe.	Europe.	North America.	North America.	Europe.	North America.	South America.	Australia.	Australia.	America.	Australia.	America.
I. Allotheria.															
1. Tritylodontidae	—		—												
2. Plagiaulacidae	—				—	—	—	—	—						
3. Polymastodontidae									—						
4. Polydolopidae										—					
II. Diprotodontia.															
1. Caenolestidae										—					
2. Phalangeridae											—	—		—	
3. Phascolomyidae												—		—	
III. Polyprotodontia.															
1. Dromatheriidae		—													
2. Triconodontidae				—	—	—									
3. Myrmecobiidae														—	
4. Peramelidae												—		—	
5. Notoryctidae														—	
6. Pantotheriidae				—	—	—									
7. Dasyuridae										—		—		—	
8. Didelphyidae							—	—	—	—			—		—
9. Caroloameghiniidae										—					

Subclass B. PLACENTALIA.

Order I. INSECTIVORA.[1]

Generally small, pentadactyl plantigrades with claws. I often enlarged in part, in other cases partly reduced. C differing but slightly from I and P: often large and two rooted or rudimentary. P acuminate, the hindermost frequently secodont. M lophodont or bunodont, the lower ones usually with five sharp tubercles, the upper tri- or quadritubercular; milk dentition usually shed early and seldom functional. Brain small with smooth hemispheres. Clavicle almost always developed.

The typical insectivores are small terrestrial animals, frequently subterranean, burrowing and nocturnal in their habits, more rarely arboreal or swimming, and subsisting on insects and worms. They form the most primitive order among *Placentalia*, and are distantly related to the polyprotodont marsupials, at least to the *Pantotheriidae*. At present several absolutely extinct forms are classed as insectivores, which frequently attain considerable size, and which formerly were attributed to the primates, or were placed in an order by themselves.

At present, the insectivores inhabit only the Old World and North America, not being found in South America or Australia. The fossil forms have practically the same distribution, one genus only being confined to South America. They begin with quite a number of extinct types in the Eocene and Oligocene of North America, but play a very insignificant part in the later Tertiary of that region, whereas in Europe they are not uncommon, in spite of their small size, from the Oligocene to the Upper Miocene.

The skull is distinguished by its low, flat outline, by the broad occiput, by the usually well-developed facial bones, by the orbits generally opening posteriorly, by the incomplete ossification of the auditory capsule, by the ring-like tympanum and by the small brain-cavity. The cerebral hemispheres are smooth; the zygomatic arch is frequently reduced. The lumbar region often has intercentra. The humerus has as a rule an entepicondylar foramen. Ulna and radius remain separated, whereas tibia and fibula are frequently fused distally. The femur has sometimes a third trochanter. The plantigrade hand almost always has five, very seldom four fingers. The hallux disappears at times. Among the burrowing forms the bones of the fore-limb are very highly specialised.

The jaw contains all of the several varieties of teeth, but the *C* and front *P* are often hard to distinguish. The normal dentition $\frac{3.1.4.3.}{3.1.4.3.}$ is often reduced. The *I* are sometimes very long, almost rodent-like and having secondary tubercles. *C* not infrequently has two roots. The number of *M* is never more than three. The last *P* frequently becomes molariform. *M*

[1] *Dobson, G. E.*, Monograph of the Insectivora, systematical and anatomical. London, 1882-90.—*Gaillard, C.*, Mammifères miocènes. Arch. Mus. Hist. Nat. Lyon, vol. vii., 1899.—*Gregory, W. K.*, The Orders of Mammals. Bull. Amer. Mus. Nat. Hist., vol. xxvii., 1910.—*Leche, W.*, Zur Entwicklungsgeschichte des Zahnsystems der Saugetiere. Bibliotheca Zoologica, Bd. xv. 1902; Bd. xx., 1907.—*Matthew, W. D.*, The Carnivora and Insectivora of the Bridger Basin, Middle Eocene. Mem. Amer. Mus. Nat. Hist., 1909.—A Zalambdodont Insectivore from the Basal Eocene. Bull. Amer. Mus. Nat. Hist., 1913.—*Osborn, H. F.*, American Eocene Primates and the Mixodectidae. Bull. Amer. Mus. Nat. Hist., 1902.—*Schlosser, M.*, Beitr. Paläontol. Österr.-Ung., Bd. vi., 1887.

are secodont, the upper ones mostly tritubercular, seldom quadritubercular, their tubercles separate or connected by ridges. The lower *M* consist of a three-pointed trigonid and of a low, often very small two-rooted talonid. The change of teeth often occurs in the embryonic stage, whereas in one genus the milk teeth are retained for a long time. The *Insectivora* may be divided into two groups: the *Menotyphla*, in which the pelvic symphysis is formed by both pubes and ischia, and the *Lipotyphla*, among which a symphysis is either lacking or is formed only by the pubes. To the *Menotyphla* belong the *Tupaiidae*, recent in eastern Asia, and the African *Macroscelididae*. Of these fossil forms are not certainly known.

The *Lipotyphla* are divided into *Zalambdodonta* and *Dilambdodonta*, to which are now attributed several extinct families, which show affinities with primates, creodonts and rodents.

Suborder A. ZALAMBDODONTA Gill.

Upper M mostly pseudo-tritubercular. Lower with strong trigonid and very much reduced talonid. Symphysis pubis reduced or wanting.

Family 1. Chrysochloridae.

This family, now native in South Africa and specialised like the moles, but having hypsodont *P* and *M*, is supposed to have one representative, namely, *Xenotherium* Douglass, in the Oligocene (White River beds) of North America.

Family 2. Necrolestidae Scott.[1]

Necrolestes Ameghino (Fig. 60). $\frac{4.1.3.3.}{4.1.3.3.}$ *I* small, *C* normally developed, P_2 two-rooted in both jaws, the lower with protocone and paracone, the rest hypsodont and tritubercular like *M*. In respect to skull, dentition and specialisation of the extremities very like the South African *Chrysochloridae*, but with longer snout. Upper Miocene of Santa Cruz, Patagonia.

Fig. 60.

Necrolestes patagonicus Ameghino. *a*, skull; *b*, humerus. 1/1. Upper Miocene of Santa Cruz, Patagonia. (After Scott.)

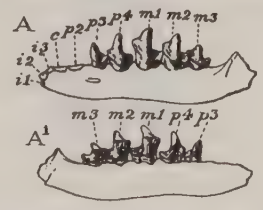


Fig. 61.

Micropternodus borealis Matthew. Lower White River beds of Oligocene; Montana. Exterior and interior aspect of mandible. 2/1. (After Matthew.)

Family 3. Centetidae.

This family is now restricted to Madagascar, with the exception of a recent genus *Solenodon* of Cuba, and closely related to the West African *Potamogalidae*. Oligocene (White River beds); Montana.

[1] Rept. Princeton University Exped. to Patagonia, vol. v. part ii., 1905.

Micropternodus Matthew (Fig. 61). $\frac{\quad}{3.1.3.3.}$ *M* composed of high trigonid and small talonid as in the case of *Centetes*.

Apternodus Matthew. $\frac{2.1.3.3.}{2.1.3.3.}$ Talonid very much reduced. P^4 in both jaws M-like. Skull like that of *Ericulus* but distinguishable by the strongly-developed mastoid.

Suborder B. DILAMBDODONTA Gill.

Upper M tritubercular, often with hypocone. Lower M tuberculo-sectorial, with well-developed talonid. Symphysis pubis small or wanting.

Family 1. Leptictidae Cope.

$\frac{2\text{-}3.1.4.3.}{2.1.4.3.}$ *Upper M very broad, triangular and tritubercular, usually with weak hypocone. Outer tubercles conical. I pointed, not unlike C. P_4 in both jaws M-like. Skull usually with two temporal crests, slender zygomatic arch and a pointed and fairly long snout. Humerus with entepicondylar foramen.*

Diacodon Cope. *Palaeictops* Matthew. Lower Eocene (Wasatch beds) of North America. A single sagittal crest on skull. *Phenacops* Matthew. Middle Eocene (Bridger).

FIG. 62.

Leptictis haydeni Leidy. Oligocene of Dakota. Upper, lateral, and lower aspect of skull. 1/1. (After Leidy.)

Leptictis, *Ictops* Leidy (Fig. 62). Skull with two temporal crests. Oligocene (White River beds); North America.

Family 2. Talpidae. Moles.

$\frac{3\text{-}2.1.4\text{-}3.3.}{3\text{-}1.1.4\text{-}3.3.}$ *Upper M tritubercular, outer tubercles V-shaped. Snout very much elongated, zygoma slender. Bullae osseae rounded. Fore-limb developed as broad, shovel-like implement. Tibia and fibula distally joined. Pelvis very long. Short tail.*

The *Talpidae* are small, underground, burrowing animals with small eyes and long snout. In the case of the mole the manubrium reaches below the second cervical vertebra and in the front includes the short almost quadrangular (square) collar-bone, which articulates with the distal end of the short, very broad humerus, and which is joined to the slender, elongated scapula by bands. The humerus has a broad, projecting deltoid ridge and next to each condyle a spur-like process. *Amphidozotherium* Filhol is found in the Oligocene Phosphorites of Quercy, and the genera *Scaptonyx* M. Edwards,

Fig. 63.

Talpa meyeri Schlosser. Lower Miocene; Weisenau, near Mainz. Humerus: *a*, internal aspect; *b*, posterior aspect; *c*, external aspect; *d*, anterior aspect; *e*, inferior aspect. 1/1. (After Schlosser.)

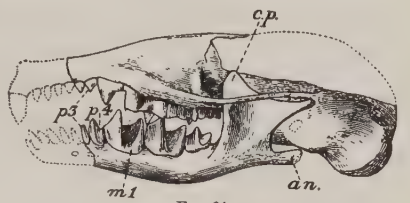


Fig. 64.

Proscalops miocaenus Matthew. Miocene of Colorado. Skull and mandible. 2/1. (After Matthew.)

Proscapanus Gaillard, and *Talpa* Linn. (Fig. 63) in the European Miocene, the latter also in the Pliocene and Pleistocene. One form also in the Miocene of Montana.

Proscalops Matthew (Fig. 64). *I* enlarged. *P*, with the exception of P^4, are small. Teeth lower than in the case of *Scalops*. Skull very broad in the rear. Lower Miocene; Colorado.

Domnina Cope. Oligocene (White River beds); North America.

Nyctitherium (*Talpavus*, *Nyctilestes*) Marsh. Upper *M* with well-developed hypocone. Middle Eocene; Bridger beds of North America.

Entomacodon (*Centracodon*) Marsh. *Myolestes* and *Entomolestes* Matthew. Same horizon and locality.

Echinogale Pomel. Lower Miocene of France. Systematic position uncertain.

Family 3. **Soricidae.** Shrew-mice.

The shrews are distinguished by strong *M*, quadritubercular in the upper jaw, and by the enlarged foremost *I*. Upper *I* is hook-like, lower horizontally placed and with sharp or jagged upper ridge. The teeth between this *I* and $M\ ^{4\text{-}6}_{2}$ are, with the exception of P^4, but slightly differentiated; the limb-bones, however, are very much specialised. Remains of *Soricidae* are found in Europe from the Oligocene on, in the Phosphorites of Quercy, in the Lower Miocene of Ulm and Mayence, in the Upper Miocene of La Grive St. Alban, and in the Pleistocene. They belong to the genera *Sorex* Linn. (Fig. 65), *Crocidura* and *Crossopus* Wagler.

Fig. 65.

Sorex pusillus Meyer. Miocene of La Grive St. Alban, Isère. Interior aspect of mandible. 1/1 and 2/1. (After Depéret.)

Protosorex Scott. Oligocene (White River beds); North America.

Family 4. Dimylidae.

$\frac{2}{2}$ *M, of which* M_1 *is very large in both jaws. I, C, P, with the exception of* P_4*, very simple. Humerus like that of Talpa.* Known only from the European Miocene.

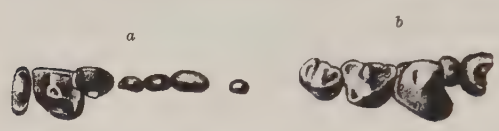


Fig. 66.

Cordylodon haslachensis v. Meyer. *a*, upper dentition; *b*, lower dentition. $^3/_1$. Lower Miocene of Ulm.

Dimylus and *Cordylodon* Meyer (Fig. 66). The latter with button-like *P*. Lower Miocene.

Plesiodimylus Gaillard, and *Metacordylodon* Schlosser in the Upper Miocene.

Family 5. Erinaceidae. Hedgehogs.

Upper M usually quadritubercular and quadrangular. P^4 *M-like, the remaining P simpler.*

Subfamily 1. Gymnurinae.

$\frac{3.1.4.3.}{3.1.4.3.}$ *C powerful.*

Necrogymnurus (*Cayluxotherium*) Filhol (Fig. 67). Phosphorites of Quercy. *Tetracus* Aymard. Oligocene; Ronzon.

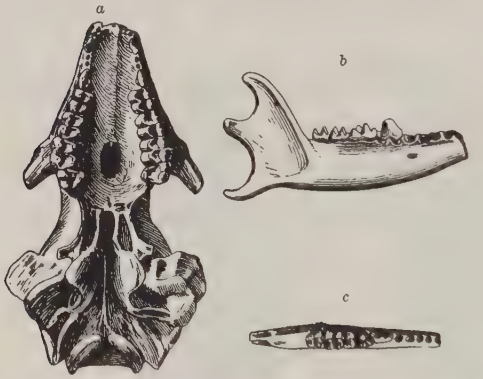


Fig. 67.

Necrogymnurus cayluxi Filhol. Phosphorites of Quercy. *a*, inferior aspect of skull; *b*, lateral aspect of lower jaw with 3 molars and P_4; *c*, superior aspect of same. $^1/_1$ (after Filhol).

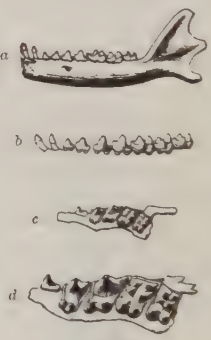


Fig. 68.

Galerix exilis Blv. sp. (*Parasorex socialis* H. v. Meyer.) Miocene of Steinheim, Württemberg. *a*, lower jaw, $^1/_1$; *b*, teeth of lower jaw enlarged; *c*, upper jaw from La Grive St. Alban, $^1/_1$; *d*, same enlarged. (After Depéret.)

Galerix Pomel (*Parasorex* v. Meyer) (Fig. 68). Upper Miocene of Europe.

Subfamily 2. Erinaceinae.

With less than $\frac{4}{4}$ *P.*

Erinaceus Linn. $\frac{3.1.3.3.}{2.1.2.3.}$ Anterior *I* enlarged, the rest, as are also *C* and M^3 reduced. Upper Miocene to recent times.

Palaeoerinaceus Filhol. Lower Miocene.

Proterix Matthew. $\frac{\quad}{3.1.3.3.}$ Oligocene (White River); South Dakota.

Family 6. **Adapisoricidae** Lemoine.

Small extinct and little-known Insectivora with 2 I, 1 C, 4 P, 3 M in the lower jaw. Upper M are tritubercular. Lower I small and rodent-like. C small. P two-rooted with principal (primary) cusp and talonid. M with high, three-pronged trigonid and strong grooved talonid. Systematic position absolutely uncertain.

Adapisorex and *Adapisoriculus* Lemoine in the Lowest Eocene of Cernay and Ay near Rheims.

Family 7. **Hyopsodontidae** Schlosser.

$\frac{3.1.4.3.}{3.1.4.3.}$ *Skull low, snout fairly long, with broad brow and occiput. Upper M square, with six tubercles, lower quadritubercular, trigonid scarcely higher than talonid. All front teeth with single cusp, almost forming a closed series, with gradual transitions from one to the next. Upper* P^2 *to* P^4 *with inner cusps, lower* P_4 *very complicated.*

This extinct family was, until very recently, placed among the *Primates* on account of the similarity of the dentition. The skull, however, shows many similarities to that of *Erinaceus*, and the metapodials also do not have button-shaped, but keeled articular facets. Also the pollex and hallux are not opposable. Connected with the small *Mioclaenidae*.

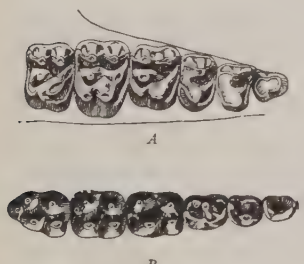


Fig. 69.

Hyopsodus paulus Leidy. Middle Eocene; Bridger beds of Wyoming. *A*, Inferior aspect of upper molars, $^2/_1$. *B*, Superior aspect of lower molars, $^2/_1$.

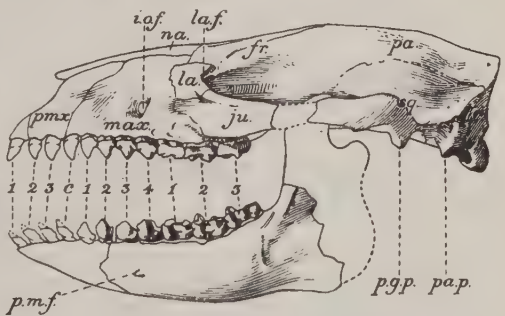


Fig. 70.

Hyopsodus decipiens Matthew. Bridger beds of Middle Eocene; Wyoming. Skull and mandible. $^1/_1$. (After Matthew.)

Hyopsodus Leidy (*Lemuravus* Marsh) (Figs. 69, 70). *I*, *C* and the front *P* are pointed and cone-shaped, P^3 and P^4 with large, thick-set outer cusps and V-shaped inner cusps. Upper *M* with two angular outer tubercles, two V-shaped inner tubercles, and two well-developed median tubercles. Lower P_4 with large median cusp and two-ridged talonid. Lower *M* with four blunt indistinctly alternating tubercles and a small hind tubercle. The orbit is on the side of the broad skull; the tympanic does not form an ossified bulla. Humerus with entepicondylar and supratrochlear foramina. Limb-bones like those of *Erinaceus*. Astragalus with flat trochlea. Terminal phalanges small, rounded, and not divided. Numerous species in the Eocene of North America. From Wasatch beds, *H. lemoinianus, miticulus* Cope.

From Wind River beds, *H. wortmani* Osborn. From Bridger beds, *H. paulus, minusculus* Leidy. From Uinta beds, *H. uintensis* Osborn.

Family 8. **Mixodectidae** Cope (*Proglires* Osborn).

$\frac{3\text{-}1.1.3.3.}{3\text{-}1.1.2.3.}$ *Upper M not much broader than long, with conical outer and small median tubercles, V-shaped protocone and weak hypocone. Lower and upper* I_1 *enlarged and forwardly inclined.* I_2 *and* I_3 *usually reduced or absent;* P_1 *and* P_2 *likewise reduced or wanting;* P_3 *and* P_4 *trenchant;* P^4 *at first with two tubercles, later becoming complicated. Lower M with five indistinctly alternating cusps, the two inner ones conical, protoconid and hypoconid V-shaped. Paraconid developed only as an edge. Trigonid not much higher than talonid, which becomes very large in the case of* M_3.

The *M* are very like those of the *Anaptomorphidae*, wherefore the *Mixodectidae* were formerly placed among the *Primates*. On account of the enlarged I_1 and the reduction of the remaining *I* and the foremost *P*, Osborn took these animals for ancestors of the rodents and called them *Proglires*. Because of the similarity of the *M* with those of *Hyopsodontidae* it might be recommended that they likewise be placed only temporarily in the insectivores, although a certain relationship with the *Primates—Chiromys*—does not seem to be excluded.

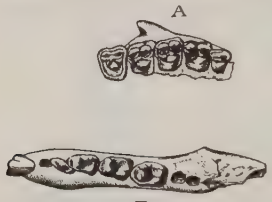


Fig. 71.

A, *Microsyops gracilis* Leidy. Upper jaw. *B*, *M. elegans* Marsh. Lower jaw. Bridger beds of Middle Eocene; Wyoming. 1/1. (After Wortman.)

Olbodotes Osborn. With three lower *I*. Lower Eocene. Torrejon beds; New Mexico. *O. copei* Osborn. A similar *M* also known from the Fort Union beds of Montana.

Mixodectes Cope. I_1 much enlarged; P_3 frequently present. Trigonid higher than talonid. Same formation and locality. *M. pungens* Cope.

Microsyops Leidy (Fig. 71) (*Limnotherium, Bathrodon, Mesacodon* Marsh, *Palaeacodon* Leidy). Talonid almost as high as trigonid. Wind River beds, *M. scottianus* Cope. Bridger beds, *M. gracilis* Leidy, *M. speciosus* Marsh.

Indrodon Cope. 2.1.3.3. Only upper jaw known. *P* simple. Lower Eocene. Torrejon beds.

Cynodontomys Cope. *C* small. P_4 *M*-like. Lower Eocene. Wasatch beds. *C. latidens* Cope.

Smilodectes Wortman. P_4 short. Middle Eocene (Bridger beds). *S. gracilis* Marsh.

Metolbodotes Schlosser. With three *I*. Tubercles of *M* inwardly connected with one another. $M_1 > M_2$ and $M_2 > M_3$. Oligocene; Fayum, Egypt. *M. stromeri* Schlosser.

Family 9. **Plesiadapidae** Lemoine.

$\frac{2.1.2.3.}{1.0.2.3.}$ *Lower jaw high with broad coronoid process and diastema behind the enlarged I. Upper* I^2 *bicuspidate,* I^3 *and C small. Upper P and M tuberculate.*

Lower M tuberculo-sectorial with fairly high trigonid and large, low talonid. Lower Eocene of Europe.

The shape of the lower jaw and the nature of the dentition indicate that we probably have to deal with the ancestral stock of rodents.

Plesiadapis Lemoine. Lower Eocene of Rheims and Belgium, possibly also in the Bohnerz of Egerkingen.

Protoadapis Lemoine. $\frac{2.1.3.3.}{}$ Without diastema. Eocene of Rheims, France. Systematic position uncertain.

Family 10. **Pantolestidae** Matthew.

$\frac{3.1.4.3.}{3.1.4.3.}$ *C normal. Upper I isolated, P simple and trenchant. Upper M tritubercular, lower tuberculo-sectorial with tricuspidate trigonid and talonid. Snout short and broad, cranium long and wide, with high supraoccipital crest and weak sagittal crest, without ossified bulla.*

The *Pantolestidae* were at first considered as *Artiodactyla*. Matthew now classes the type species as insectivore on account of the characters of the skeleton, the presence of a mental foramen below *M*, and the short, broad snout. Were it not for these characteristics they might also be placed under the head of creodonts. The much-curved humerus has a well-developed deltoid crest and an entepicondylar foramen, the femur has a third trochanter, and tibia and fibula are distally co-ossified. The astragalus has a broad, furrowed trochlea and a short neck, the claws are flattened and broad. The tail is rather long. The extremities show adaptation to aquatic life.

Pantolestes Cope (*Passalacodon*, *Anisacodon* Marsh). Paraconid small. Middle Eocene (Bridger beds).

Palaeosinopa Matthew. Paraconid well developed. Lower Eocene (Wasatch beds).

Pentacodon Scott. Lower Eocene (Torrejon beds); New Mexico.

? *Ptolemaia* Osborn. Paraconid weak. *I* and foremost *P* reduced. Oligocene; Egypt.

Family 11. **Tillodontidae** (*Tillodontia* Marsh).[1]

Extinct, pentadactyl, clawed plantigrades with enlarged and rodent-like I_2 *and brachyodont M. Upper M tritubercular, with secondary tubercles, lower with high semicircular? trigonid and a somewhat lower semicircular talonid. Scaphoid separated from lunar.*

The skull is on the whole carnivore-like. The breadth of snout and occiput, the lack of postorbital contraction and the nature of the auditory region—flat bulla—as well as the shape of the articulation of the mandible emphasise the connection of this family with the insectivores. The differentiation between *I* and *C* also agrees with this interpretation. The first pair of *I* are lost, the second pair enlarged, the *C* pass into small intermediate teeth, and accordingly the hinder *P* become *M*-like.

[1] *Cope, E. D.*, Vertebrata of the Tertiary formations of the west, 1877.—Tertiary Vertebrata, 1884.—*Gregory, W. K.* Bull. Amer. Mus. Nat. Hist., 1910, p. 292.—*Marsh, O. C.* Amer. Journ. Sci., 1875, vol. ix.; 1876, vol. xi.

The principal bones of the skeleton are known in *Tillotherium*, but it is only partially known in *Esthonyx*. Only in the Eocene of North America and England.

Fig. 72.

Esthonyx burmeisteri Cope. Lower Eocene; Wasatch beds of Big Horn, Wyoming. *A*, Upper dentition. *B*, Lower dentition showing chewing surface. $^2/_3$ (after Cope).

Subfamily 1. Esthonychinae.

$\frac{2.1.3.3.}{3.1.3.3.}$ *I entirely covered with enamel, with roots. C rather large.*

Esthonyx Cope (Fig. 72). In Lower Eocene Wasatch beds of Wyoming and New Mexico.

Platychoerops Charlesworth in London Clay of England.

Plesiesthonyx Lemoine. Lower Eocene of Rheims. Position doubtful.

Subfamily 2. Tillotheriinae.

$\frac{2.1.3.3.}{2.1.2.3.}$ *Upper and lower* I_2 *well developed, enamelled only on the anterior face and with persistent pulp. Small diastemata between I, small C and the most anterior P.*

Fig. 73.

Tillotherium fodiens Marsh. Bridger beds of Eocene; Wyoming. Skull and mandible. $^1/_4$. (After Marsh.)

Tillotherium Marsh (Fig. 73). Skull the same size as that of bear with small cranial cavity and slender snout. The orbits are not separated posteriorly from the temporal fossa. Frontal large, with air cells. The vertebrae are like those of the predaceous animals. Humerus with entepicondylar foramen. Femur with third trochanter. Fibula slender, astragalus low. Middle Eocene. Bridger beds; Wyoming.

Trogosus (*Anchippodus*) Leidy. Same horizon and locality.

Order II. CHIROPTERA. Bats.[1]

Small, insectivorous, seldom frugivorous, animals with very long fore-limbs, with digits joined by a wing-membrane. Dentition complete, I reduced, C large, generally with strong basal ridge, P pointed. M secodont or bunolophodont, upper M tritubercular with V-shaped tubercles, lower M tuberculo-sectorial. Milk-teeth rudimentary. Brain small and smooth. Two mammae in pectoral region.

The bats form a specialised group of primitive insectivores. They are distinguished from the true insectivores not only by the peculiar development of their fore-limbs, but also by the generally shorter snout, the well-developed sagittal crest, the marked postorbital constriction and the completely ossified auditory bulla.

The fore-limb is changed into an organ of flight (Fig. 74). The long clavicle joins the sternum with the acromion of the shoulder-blade. The

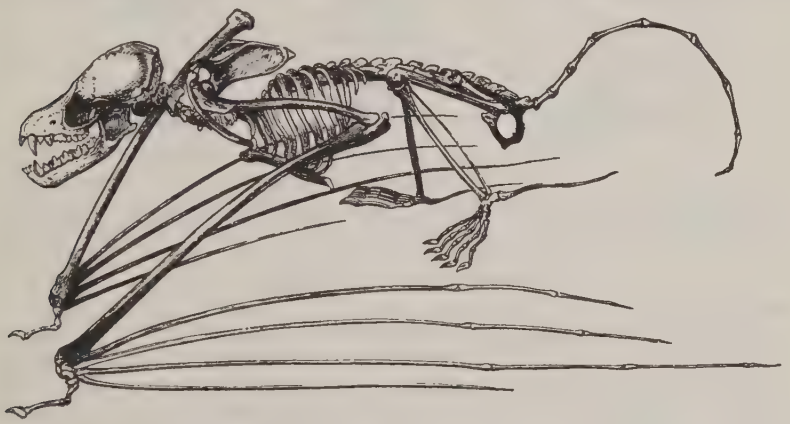


FIG. 74.

Vespertilio murinus Linn. Skeleton. (After Blainville.)

humerus is slender and, in comparison with the size of the caput and the deltoid ridge, very long. The length of the forearm exceeds that of the upper arm, as a rule, by a third, often, however, it is twice as long. The ulna is very much reduced. The proximal carpalia are fused. The phalanges, with the exception of the short, opposable thumb, become long, exceedingly delicate structures, and are united with skin, which is also attached to the hinder part of the body, to the tail, and to a long, ossified spur, extending from the calcaneum. In contrast to the fore-limb, the hind-limb and pelvis are weakly developed. The pes is pentadactyl, and the digits, all of equal length, are clawed.

Bats are divided into two groups: (1) *Megachiroptera*, which consist only of large frugivorous forms, and (2) the small, insectivorous *Microchiroptera*.

[1] *Gaillard, C.*, Mammifères miocènes de La Grive St. Alban. Arch. Mus. Hist. Nat. Lyon, vol. vii., 1899.—*Schlosser, M.*, Die Affen, Lemuren, und Chiropteren des europäischen Tertiärs. Beitr. Paläontol. Österr.-Ung., vol. vi., 1887.—*Weithofer, A.* Sitzber. Wien. Akad., math. phys. Cl. Bd. xcvi., 1887.—*Winge, H.*, Jordfundne og nulevende Flagermus (Chiroptera) fra Lagoa Santa. E. Museo Lundii. Kjøbenhavn, 1892.

The genus *Archaeopteropus* Meschinelli from the Oligocene of Monteviale probably belongs to the *Megachiroptera.*

Remains of *Microchiroptera* have been found in large quantities only in the Phosphorites of Quercy, the Pleistocene in European and Brazilian caves, but these Pleistocene remains belong almost exclusively to recent forms. In the Eocene of Paris and Aix, and also in the Miocene, remains of bats are very rare, with the exception of the locality of La Grive St. Alban.

The *Chiroptera* from the Phosphorites comprise the following genera: *Pseudorhinolophus* (Fig. 75) and *Vespertiliavus* Schlosser, *Taphozous* Geoffr., *Alastor* and *Necromantis* Weithofer, the latter of which is closely related to living South American forms, which is also true of *Provampyrus* Schlosser from the Oligocene of Egypt. In the Miocene, besides the extinct genus *Palaeonycteris*, there are the living genera *Vespertilio*, *Vesperugo*, *Rhinolophus*, and *Cynonycteris.*

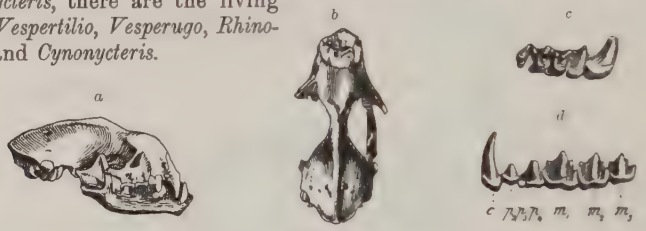


FIG. 75.

Pseudorhinolophus sp. Phosphorites of Quercy. *a*, lateral aspect of skull with lower jaw, $^1/_1$; *b*, superior aspect of same, $^1/_1$; *c*, inferior aspect of upper dentition, enlarged; *d*, lateral aspect of lower dentition, enlarged. (After Schlosser.)

Order III. CARNIVORA.

Carnivorous mammals include a great variety of extinct and recent forms; some of which are aquatic, but the majority are of terrestrial habit, mostly of moderate size, but varying considerably in this respect. The dentition is regularly diphyodont and heterodont, the teeth always rooted; incisors usually $\frac{3}{3}$, canines always $\frac{1}{1}$, strong, pointed, recurved. Cheek teeth more or less sectorial, posterior molars generally flattened and tuberculated, never compound. The milk dentition is invariably complete.

In all recent forms the brain is of moderate capacity, with strongly convoluted hemispheres; but in the earliest fossil forms (*Creodontia*) it is smaller and nearly smooth. The feet have never less than four well-developed digits, and a fifth may be present; they are unguiculate, the claws being more or less pointed, rarely rudimentary or absent, and may be either plantigrade, digitigrade, or, as in the seals, modified into flippers. Three suborders are recognised, namely, *Creodontia*, *Fissipedia* and *Pinnipedia.*

Suborder A. CREODONTIA. Primitive Carnivora.[1]

Extinct digitigrade or semiplantigrade carnivores with small weakly convoluted cerebrum. Dentition generally $\frac{3.1.4.3.}{3.1.4.3.}$. *Molars trenchant or tubercular, more or less*

[1] *Cope, E. D.*, The Creodonta. American Naturalist, 1884, pp. 255-478. — *Filhol, H.* Ann. Soc. Géol., 1872, vol. iii.; 1876, vol. vii.; 1877, vol. viii. — Ann. Soc. Sci. Phys. Nat. Toulouse, 1882. — *Martin, R.*, Revision der Creodonten Europas. Revue Suisse Zool. Genève, 1906. — *Matthew, W. D.*,

uniform. Auditory bulla rarely ossified. Tail long. Scaphoid, centrale and lunar usually distinct. Astragalus gently convex superiorly, smooth or only slightly grooved. Terminal phalanges generally broad, obtuse and cloven, flattened inferiorly, more rarely pointed and laterally compressed. Seven lumbar and twelve dorsal vertebrae; lumbar vertebrae with cylindrical prezygapophyses.

The group *Creodontia*, as first separated by Cope from the *Carnivora vera*, exhibits genetic relations with the *Marsupialia* as well as with the *Fissipedia*, with which they may be united through the family *Miacidae*, having in common the development of the fourth premolar above and the first molar below as carnassial teeth.

The skull is of the usual carnivore type, large when compared with the trunk and limbs, and having the snout elongated. The cranial cavity is remarkable for its small size, and its narrow elongated form, the auditory bulla being only exceptionally ossified. The brain is diminutive, and with but few, faint convolutions. There are no vacuities in the palate as in carnivorous marsupials, although numerous small perforations may exist. Only rarely, as in the *Mesonychidae*, etc., are the posterior angles of the lower jaw somewhat inflected.

The dentition exhibits the normal formula $\frac{3.1.4.3.}{3.1.4.3.}$, but the incisors, premolars, and molars may become reduced in number although not all simultaneously. The dentition differs from that of the carnivorous marsupials in having fewer incisors, which increase in size from the first onwards; and from the insectivores in that these teeth are more compactly arranged. The canines are strongly developed, conically pointed, and always single-rooted. The premolars are distinguished from the molars by their greater simplicity and compression, the most posterior frequently simulating morphologically a true molar, but not developed in the upper jaw as a carnassial tooth like that of the *Fissipedia*. Excepting in the *Miacidae*, the first lower molar is not enlarged more than the others, or otherwise differentiated, and if anything, is smaller than the immediately adjoining teeth. The crowns of the superior molars are invariably tritubercular, consisting of two outer and one inner cusp, the latter generally being united to the former by V-shaped crests. They may undergo great changes, the parastyle and metastyle becoming very strong.

The inferior molars are normally tuberculo-sectorial, with pitted talonid; the metaconid may be very faint or even wanting, while the trigonid becomes shear-like, or sometimes reduced. In contrast to the true carnivores the first lower molar is generally smaller than the succeeding teeth, either the second or third being the largest. The antepenultimate milk molar resembles the last permanent premolar.

In comparison with the length of the cranium, the extremities are usually shorter than in recent carnivores, and as a rule, stouter and more

Additional observations on the Creodonta. Bull. Amer. Mus. Nat. Hist., 1901.—The Osteology of Sinopa. Proc. U.S. Nat. Mus., vol. xxx., 1906.—The Carnivora and Insectivora of the Bridger Basin. Mem. Amer. Mus. Nat. Hist., 1909.—*Osborn, H. F.*, and *Wortman, J. L.* Bull. Amer. Mus. Nat. Hist., N.Y., 1892; 1900.—*Schlosser, M.*, Die Affen, Creodonten, etc., des europäischen Tertiärs. Beiträge z. Paläont. Österr.-Ung., 1887, vi.—*Scott, W. B.* Journ. Acad. Nat. Sci. Philad., 1887–95—Proc. Acad. Nat. Sci. Philad., 1892.—*Wortman, J. L.* Bull. Amer. Mus. Nat. Hist., N.Y., 1894, 1899.—Eocene Mammalia in the Marsh Collection. I. Carnivora. Amer. Journ. Sci., 1901, 1902.

compact. The humerus invariably has an entepicondylar foramen, and an undivided distal trochlea, which in higher forms extends as far back as the olecranon fossa.

The radius, ulna and usually all of the carpal bones remain distinct, but in the *Arctocyonidae* the scaphoid and centrale are united. Fusion between these bones and the lunar, which is exceedingly common in the true carnivores, occurs exceptionally, and perhaps not at all in some of the later species of *Hyaenodon*.

The metacarpals correspond in form, size and arrangement with those of recent carnivores. The distal phalanges may become elongated or even hoof-like (*Pachyaena*). The ilium is triangular, resembling that of the insectivores and marsupials, and more slender than that of true carnivores; the femur has a more or less conspicuous third trochanter. The tarsal bones agree essentially in form and arrangement with those of recent members of the order, differing in that the astragalus and calcaneum are more compact and less closely apposed.

According to Matthew's classification, the *Creodontia* may be divided into three groups, *Acreodi*, *Pseudocreodi* and *Eucreodi*, the latter being the point of transition to the *Carnivora vera*.

Tribe 1. ACREODI.

Molars not of trenchant form, primitive; superiorly tritubercular, inferiorly with blunted cusps.

Family 1. **Oxyclaenidae** Scott.

No specialised carnassial, superior molars tritubercular, subquadrate or triangular in outline; inferior molars tuberculo-sectorial with angular cusps, trigonid higher than talonid. P^1 simple, P^4 occasionally simple, P^3 with internal cusp.

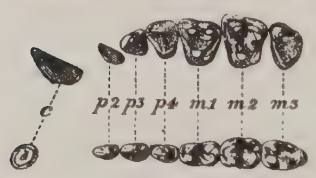


FIG. 76.

Tricentes subtrigonus Cope. Torrejon beds of Lower Eocene; New Mexico. Upper and lower dentition. 1/1. (After Matthew.)

The skeleton is but little known, and generic distinction is based entirely on dental characters. From the early Eocene of New Mexico, Wyoming, and Montana.

Oxyclaenus, *Loxolophus*, *Carcinodon* Cope. *Protochriacus* Scott. *P* 4/4. All from the Puerco beds.

Chriacus, *Tricentes* Cope (Fig. 76). Torrejon and Ft. Union beds, associated with *Deltatherium*. *P* 3/3.

Family 2. **Mesonychidae** Cope.

$\frac{3-2}{3}$ *M. No carnassials, superior molars and last premolar tritubercular with high, blunt-topped cusps. Lower jaw with cusps of teeth arranged serially, the central cusp much the highest, talonid usually trenchant or basin-shaped. Manus and pes paraxonic, extremities originally pentadactyl, later becoming tetradactyl. Humerus with supratrochlear foramen, fibula articulating with calcaneum, claws blunt and hoof-like. Zygapophyses of lumbar vertebrae cylindrical or inrolled. Brain very diminutive.*

The *Mesonychidae* usually attain the size of bears, and their extremities resemble those of the *Canidae*, hence they were fleet and strong runners. The carpals and tarsals are compactly set, astragalus with deeply grooved trochlea, the first digit has become atrophied, and the metapodials are parallel and digitigrade. The upper molars are distinguished by having three cusps but lacking a metastyle, and the lower by the reduction of the metaconid and the simple form of the talonid, thus being secondarily triconodont. Upper and lower molars never form a shearing surface. Distributed in the Lower Eocene of North America, France, and Belgium.

Subfamily 1. Triisodontinae Matthew.

P $\frac{4}{4}$. *M* $\frac{3}{3}$; *or P* $\frac{3}{4}$, *M* $\frac{2}{3}$. *Trigonid of lower molars with inner cusps, talonid broad, concave. Outer cusp of superior molars isolated.*

Triisodon Cope. *Eoconodon* Matthew and Granger. Puerco beds.
Sarcothraustes, Goniacodon, Microclaenodon Cope. Torrejon beds.

Subfamily 2. Mesonychinae Matthew.

Lower molars with talonid trenchant. Outer cusps of upper molars fused.

Dissacus Cope. M $\frac{3}{3}$. Anterior lower molars with strong metaconid. Humerus with entepicondylar foramen; extremities pentadactyl. Wasatch

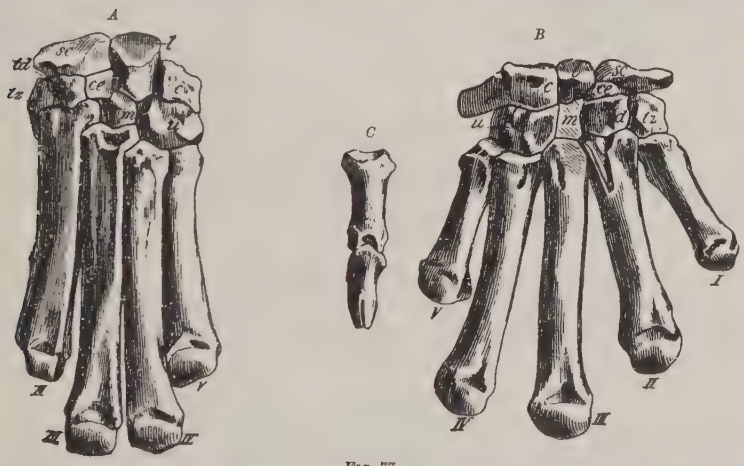


Fig. 77.

Manus of *Mesonyx* (*A*) and of *Hyaenodon* (*B*) about $\frac{2}{3}$. *sc*, Scaphoid; *l*, lunar; *c*, cuneiform; *ce*, centrale; *tz*, trapezium; *td*, trapezoid; *m*, magnum; *u*, unciforme; *I.-V.*, first to fifth metacarpals. *C*, The last two phalanges of *Hyaenodon*.

and Torrejon beds of New Mexico; Wasatch and Wind River beds of Wyoming. Basal Eocene near Rheims, France.

Hyaenodictis Lemoine. Basal Eocene of Cernays near Rheims, and Erquelinnes, Belgium.

Hapalodectes Matthew. Teeth somewhat compressed. Molars without metaconid. Wasatch and Wind River beds. Basal Eocene.

Pachyaena Cope. Dentition $\frac{3.1.4.3.}{2.1.4.3.}$. Limb bones stout, ungual phalanges hoof-like, angle of lower jaw sometimes inflected. This form attained the size of a bear. Wasatch beds of New Mexico and Wyoming. Middle Eocene; Paris Basin.

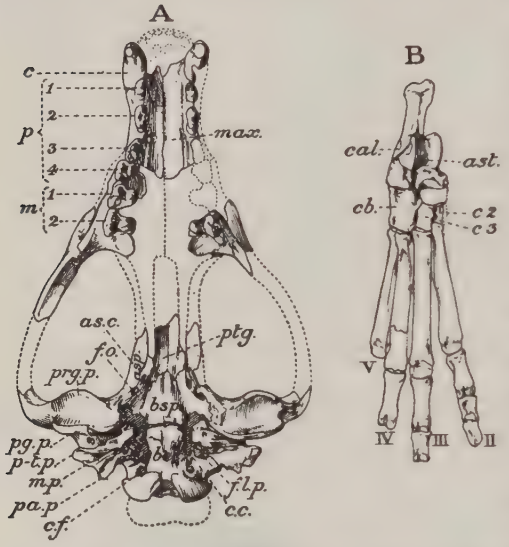


FIG. 78.

Mesonyx obtusidens Cope. Bridger beds of Middle Eocene; Wyoming. *A*, Inferior aspect of skull. *B*, Pes. 1/3. (After Matthew.)

Harpagolestes Wortman. Cranium broad and short. M^3 wanting. Humerus lacking entepicondylar foramen. *H. immanis* Matthew, about the size of a bear. *H.* (*Mesonyx*) *uintensis* Scott. Uinta Beds.

Synoplotherium Cope (*Dromocyon* Marsh). Cranium and limbs somewhat elongated; manus and pes tetradactyl, astragalus with deeply grooved trochlea. *S. lanius* Cope. *S. vorax* Marsh sp. Bridger beds.

Mesonyx Cope (Figs. 77A, 78). M^3 lacking. Humerus without entepicondylar foramen; lachrymal bone prominent. *M. immanis* Wortman. *M. obtusidens* Cope. Bridger beds.

The skeletons of *Mesonyx* and *Dromocyon* are very satisfactorily known. The claws are thick and cleft at the tips, the metapodials closely appressed as in the *Canidae*.

Tribe 2. PSEUDOCREODI.

$M \frac{1}{2}$ or $M \frac{2}{3}$ functioning as carnassials. Claws cleft, manus and pes mesaxonic. Fibula articulating with calcaneum. Zygapophyses of lumbar vertebrae cylindrical or inrolled.

Family 3. Oxyaenidae.

P^4 with inner cusp. M^2 placed transversely, M_2 usually larger than M_1. Cranium of moderate size, with broad basis cranii; mandible massive with strong symphysis. Extremities plantigrade, pentadactyl, claws more or less fissured at the tips, blunt; toes spreading in aquatic forms.

Osborn regards the genus *Palaeonictis* as ancestral to the *Felidae*, and according to Wortman *Patriofelis* stands in similar relation to the *Pinnipedia*. The researches of Matthew fail to indicate that either genus gave rise to later forms.

The third upper and lower molars became lost in this family. Reduction of M^2 is first indicated by the transverse position assumed by this tooth, which may completely disappear. Trigonid of M_1 complemented by a metastyle functioning as a blade; in the lower molars, the internal tubercles and particularly the talonid gradually become reduced, the latter even disappearing.

Subfamily 1. Limnocyoninae Wortman.

Only P^4 with inner tubercles. Inferior molars tuberculo-sectorial. $\frac{2-3}{2-3}$ *M. Dentition not reduced. Muzzle long. Small to moderate-sized forms.*

Limnocyon (*Telmatocyon*) Marsh (Fig. 79, A). I^3 reduced, $\frac{P^1}{P_1}$ two-rooted. P^4 with inner tubercle. Of the superior molars M^1 with strong protocone, M^2 is transversely placed. M_1 and M_2 with well-developed trigonids, and concave talonid. Limbs short, somewhat bowed. Bridger beds.

Thinocyon Marsh. Limbs long and slender. About the size of a domestic cat. Bridger beds.

Thereutherium Filhol. P single-rooted, M^2 and metaconids of lower molars reduced. Mandible stout. *T. thylacodes* Filhol. Eocene; Quercy Phosphorites.

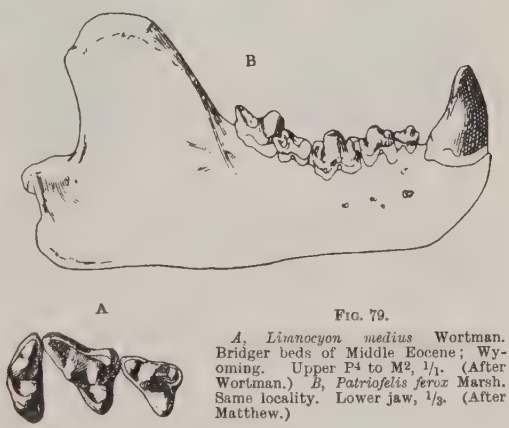


Fig. 79.

A, Limnocyon medius Wortman. Bridger beds of Middle Eocene; Wyoming. Upper P^4 to M^2, 1/1. (After Wortman.) *B, Patriofelis ferox* Marsh. Same locality. Lower jaw, 1/3. (After Matthew.)

Oxyaenodon Wortman. Dentition $\frac{3.1.4.2.}{3.1.4.2.}$. M^1 as in *Limnocyon*. P somewhat crowded and reduced. Mandible moderately high. Bridger and Uinta beds.

Machairoides Matthew. Symphysis of mandible flanged inferiorly. Bridger and Uinta beds.

Subfamily 2. Oxyaeninae Wortman.

P commonly reduced, P^3 and P^4 with inner tubercles. M^2 often lost. P and M trenchantly modified. Muzzle short. Forms early becoming specialised.

Oxyaena Cope. Dentition $\frac{3.1.4.2.}{3.1.4.2.}$. Superior premolars with inner tubercles. M^1 with well-developed protocone, M^2 transverse in position. Inferior molars with reduced talonids. Mandible deep, but not robust. Limbs moderately long. *O. lupina* Cope. Wasatch beds. *O. galliae* Filhol. Quercy Phosphorites.

Patriofelis Leidy (*Limnofelis, Oreocyon* Marsh; *Aelurotherium* Adams;

Protopsalis Cope) (Fig. 79, B). Dentition $\frac{3.1.3.1.}{2.1\ 3.2.}$. $P\ \frac{1}{1}$ lost; M^2 very small or wanting. M_1 with faint talonid and small metaconid. M_2 resembles M_1 of the *Felidae*, while M^1 may be compared to P^4 of the latter. Muzzle truncated, mandible massive, limbs short and stout, toes spreading. Possibly semi-aquatic in habits. *P. ulta* Leidy. Wasatch and Bridger beds.

Palaeonictis Blv. Dentition $\frac{3.1.4.2.}{3.1.4.2.}$. P^3 and P^4 with lower inner tubercles. M^1 with well-defined paracone and metacone, large protocone and intercalary tubercles. Inferior molars with strong paraconid and metaconid, concave talonid. M_1 larger than M_2. Wasatch beds of North America and Lower Eocene of Soissons, France.

Ambloctonus Cope. $\frac{2}{2}$ *M.* M_2 of carnassial type lacking metaconid and heel, but smaller than M_1. Wasatch beds. North America.

Family 4. **Hyaenodontidae** Cope.

$\frac{3-2}{3}$ *M.* *M* $\frac{2}{3}$ *developed as carnassial teeth.* P^4 *and anterior molars functioning as subordinate shearing teeth. Cranium usually long, less often short and stout, with concave forehead. Extremities mesaxonic, adapted for running, fibula articulating with calcaneum. Claws cleft at the tips. Auditory bulla very rarely completely ossified.*

The *Hyaenodontidae* embrace forms ranging in size from a fox to a wolf, some species attaining the dimensions of a tiger. There is a tendency towards the anchylosis of the scaphoid and lunar (Fig. 77, *B*); the humerus acquiring a stout deep trochlea and supratrochlear foramen, while pollex and hallux may undergo considerable reduction. The cranium is generally narrow and elongate, but may, as in *Pterodon*, and in many species of *Hyaenodon*, be short and broad. Of the upper teeth, M^3 may disappear, M^2 forms a shear with M_3, M^1 and P^4 function similarly with M_1 and M_2 respectively. As a result of the cutting plates so formed, only the paracone and metastyle of the upper molars remain, and the paraconid and protoconid of the lower.

Subfamily 1. Proviverrinae.

$\frac{3}{3}$ *M. Upper molars tritubercular.* M^3 *transversely placed, lower M tuberculo-sectorial, always with a metaconid. Teeth with moderate shearing surface. Body slender. Extremities with five digits, which are of nearly uniform length. Claws compressed.*

The *Proviverrinae* were approximately the size of a fox, possessing a civet-like aspect. The ancestors of most true carnivores are to be sought in this neighbourhood.

Sinopa Leidy (*Stypolophus*, *Prototomus* Cope). *P* long and remaining isolated. Outer tubercles of superior molars distinct, talonid large and basin-shaped. The extremities, apart from the non-fusion of scaphoid and lunar, resemble those of the *Viverridae*, but the symmetry of the foot is mesaxonic, and the claws are cleft. Wasatch beds. *S. hians* Cope. Bridger beds. *S. rapax* Leidy; *S. grangeri* Matthew. Possibly represented also in the basal Eocene of Belgium (Orsmael).

Tritemnodon Matthew (*Stypolophus* Cope, *Limnocyon* Marsh). External tubercles of superior molars closely connate. Talonid small, trenchant. *T. agilis* Marsh sp. Bridger beds.

Metasinopa Schlosser. Only M_1 with metaconid. Talonid trenchant. Oligocene; Egypt.

Proviverra Rütimeyer. *P* short but high. Talonid large, concave. Outer tubercles of superior molars well separated. Middle Eocene; Bohnerz of Egerkingen.

Cynohyaenodon Filhol (Fig. 80). Outer tubercles of upper molars closely approximated. Quercy Phosphorites.

Prorhizaena Rütimeyer. Known only by upper dentition, M^2 not reduced. Bohnerz of Egerkingen.

Galethylax Blainville. Calcaire Grossier; Paris basin.

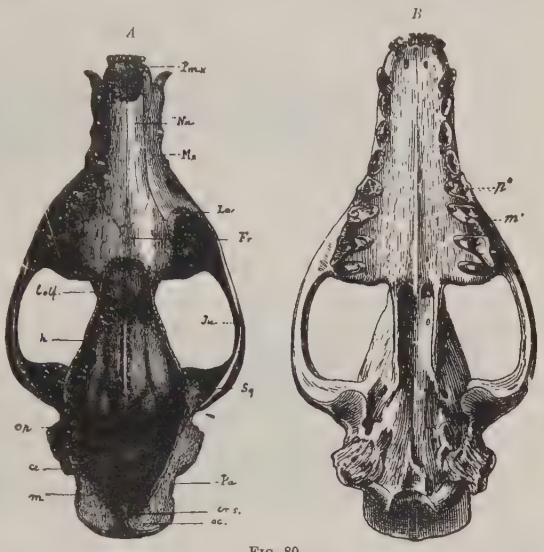


FIG. 80.

Cynohyaenodon cayluxi Filhol. Phosphorites of Quercy. *A*, *B*, Superior and inferior aspect of skull. 2/3. (After Gaudry and Filhol.) *oc*, Supra-occipital; *Pa*, parietal; *Fr*, frontal; *Ju*, jugal; *Sq*, squamosal; *La*, lachrymal; *Na*, nasal; *Mx*, maxilla; *Pmx*, premaxilla; *crs*, sagittal crest; *m*, medulla oblongata; *ce*, cerebellum; *op*, optic lobes; *h*, cerebrum; *lolf*, olfactory lobes.

Quercytherium Filhol. *P* strongly thickened. Quercy Phosphorites.

Subfamily 2. HYAENODONTINAE.

$\frac{3-2}{3}$ *M. All molars trenchant. Superior molars with prolonged metastyle and reduced paracone, at times lacking protocone. Inferior molars without metaconid, talonid small or wanting.* P_4 *higher than* M_1. *Body stout, extremities with heavy claws and adapted for running.*

The *Hyaenodontinae* are probably an offshoot of the *Proviverrinae*, from which they are distinguished by having trenchant *M.* They appear in Europe in the early Eocene, in North America and Africa in the Oligocene.

Pterodon Blainville (*Hemipsalodon* Cope) (Fig. 81). Molars $\frac{3}{3}$. M^1 and M^2 with closely compressed outer cusps and strong protocone. M^3 transversely placed. Inferior molars with high, thick protoconid, robust paraconid and rudimentary talonid. *P* simple, thickened, P_1 and lower first incisor frequently missing. Canines strongly developed. Cranium heavy, muzzle abbreviated. Calcaire Grossier of Paris; Débruge, Isle of Wight, and Quercy Phosphorites in the Upper Eocene. *P. dasyuroides* Gerv. Oligocene. *P. grandis* Cope; *P. africanus* Andrews. White River beds of Canada and Oligocene of Egypt respectively. They are the size of a tiger.

Propterodon Martin. $\frac{4}{4}$ *P.* Bohnerz of Egerkingen. Middle Eocene.

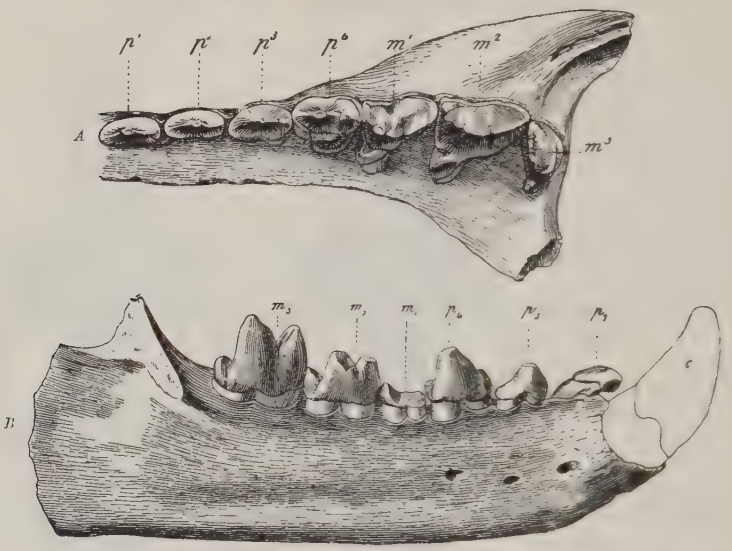


Fig. 81.

Pterodon dasyuroides Gerv. Upper Eocene; Phosphorites of Mouillac, near Caylux. *A*, Inferior aspect of left upper dentition, $^1/_1$. *B*, Exterior aspect of right mandible, $^2/_3$.

Pseudopterodon Douglass. This small form is not very well known. White River beds.

Fig. 82.

Hyaenodon leptorhynchus Laizer and Parieu. Upper Eocene; Phosphorites of Caylux. Anterior portion of skull and mandible. $^1/_2$. (After Filhol.)

Apterodon Fischer (*Dasyurodon* Andreae). Paraconid rather low, talonid large, trenchant. Each of upper molars with three prominent tubercles and faint metastyle. Cranium and muzzle elongated, extremities short and bowed, adapted for semi-aquatic existence. Quercy Phosphorites and Flonheim sand; Oligocene. *A. flonheimensis* Andreae. *A. macrognathus* Andrews, from the Oligocene of Egypt.

Hyaenodon Laizer and Parieu (*Taxotherium* Blv.; *Tulodon* Gerv.) (Fig. 82). Dentition $\frac{2.1.4.2.}{3.1.4.3.}$. Upper molars with metastyle developed as a long blade.

M^1 with more or less fused paracone and metacone and rudimentary protocone, which is lacking on M^2; M^3 wanting. M_1 and M_2 with short protoconid and rudimentary talonid, which is lacking in M_3, but the protoconid is developed as a long blade, as is the metastyle of the superior molars. Cranium and extremities long and slender, or short and thickened. Humerus with prominent trochlea; first digit often reduced. Rather abundant in the Bohnerz of Egerkingen, Upper Eocene Phosphorites, Gypsum Beds of Paris, Lignite of Débruge, Euzet les Bains (Gard). *H. requieni* Gerv. is represented by numerous varieties in the Phosphorites, and the Oligocene of Ronzon and Cournon. *H. horridus* Leidy well represented in White River Oligocene of North America.

Tribe 3. EUCREODI.

P^4 and M_1 may be developed as carnassial teeth. Claws compressed and not cleft. Manus and pes almost paraxonic. Fibula not articulating with calcaneum. Zygapophyses of lumbar vertebrae flattened.

Family 5. **Arctocyonidae** Gervais.

$\frac{3}{3}$ M. No carnassial teeth, molars low, upper molars multitubercular. Lower molars with large talonid and reduced paraconid. P simple, diminutive. Extremities plantigrade, pentadactyl. Centrale fused with scaphoid.

The *Arctocyonidae* are omnivorous creodonts, with sharp canine teeth, and resemble the *Ursidae* in many respects, apparently undergoing a similar specialisation from the Creodont stem. They occur in the basal Eocene of Rheims, and in North America in the Torrejon, Fort Union, and Wasatch beds.

Fig. 83.

Arctocyon primaevus Blainv. Lower Eocene; La Fère near Rheims. Skull. 1/3. (After Gaudry.)

Fig. 84.

Arctocyon gervaisi Lemoine. Lower Eocene; Cernays near Rheims. *A*, Inferior aspect of 3 upper molars, 1/1. *B*, Superior and lateral aspect of lower molars, 1/1. (After Lemoine.)

Arctocyon Blv. (Fig. 83). Upper molars with five to six tubercles. *C* long, slender, serrated posteriorly. Basal Eocene; Cernays, near Rheims.

Claenodon Scott (*Mioclaenus* Cope in part). Upper molars resembling preceding form, P^4 with strongly developed inner tubercle. Extremities like those of bears, but astragalus with long neck. Torrejon beds. *C. ferox*, *C. corrugatus* Cope.

Anacodon Cope. Tubercles obscure. *A. ursidens* Cope. Wasatch beds.

Family 6. Miacidae Cope.

P^4 and M_1 developed as carnassials. Upper molars tritubercular, lower molars tuberculo-sectorial with high trigonid and much reduced talonid. Extremities pentadactyl.

The *Miacidae* are small to moderate-sized carnivores, resembling in dentition partly the *Viverridae*, and the primitive *Canidae* and *Ursidae*, being doubtless the common ancestor. They may be distinguished from the latter by the absence of a bony tympanic bulla, the free scaphoid, centrale, and lunar bones, and principally by the presence of a third though small trochanter in the femur. The brain is much more developed than in other creodonts. As the skeletal structure becomes better known, it may be possible to assign here a number of European forms, such as those provisionally regarded as Eocene species of *Viverra* and *Amphicyon*.

Subfamily 1. Viverravinae Matthew.

$\frac{2}{2}$ *M. Inner cusp of P^4 and posterior cusp of P_4 large. Toes compactly set, digitigrade. Humerus with low deltoid crest, and prominent greater tuberosity. Femur with prominent elongated third trochanter. Astragalus with narrow head, and somewhat grooved trochlea. Fibula articulating with calcaneum. Cranium somewhat elongated.*

Fig. 85.

Didymictis haydenianus Cope. Puerco of Lower Eocene; New Mexico. Inferior aspect of left upper jaw with two molars and two premolars. (After Cope.)

Viverravus Marsh. Teeth compressed. Upper molars lacking median tubercles, M^1 with small hypocone. M_1 with short pitted talonid. Bridger beds. *V. dawkinsianus* Cope; *V. minutus* Wortman. These are probably present also in Upper Eocene of Quercy, France. Reported from Landenien of Erquelinnes, Belgium.

Didymictis Cope (Fig. 85). Dentition massive. M^1 lacking hypocone. M_1 with pitted talonid. Torrejon and Fort Union beds. *D. haydenianus*, *D. protenus* Cope. Wasatch and Wind River beds.

Subfamily 2. Miacinae Matthew.

$\frac{3}{3}$ *M. Inner cusps of P^4 small or wanting. Extremities plantigrade, toes spreading. Humerus with prominent deltoid crest, but small greater tuberosity. Femur with low and extended third trochanter. Astragalus with broadened head and flattened trochlea. Fibula not articulating with calcaneum. Cranium of moderate size.*

Miacis and *Uintacyon* attain the size of dogs and raccoons respectively.

Miacis Cope. P_4 and M_1 of moderate to large size, the latter with pitted talonid. M^1 generally with small hypocone, both posterior molars small. *M. parvivorus* Cope. Wasatch beds. *M.* (*Lycarion*) *hargeri* Wortman. *M.* (*Harpalodon*) *sylvestris* Marsh. Bridger beds. *M.* (*Prodaphaenus*) *uintensis* Osborn. Uinta beds. *M. exilis* Filhol sp. Phosphorites, Quercy.

Uintacyon Leidy. Posterior molars large, M^1 lacking hypocone; P and M_1 small, the latter with trenchant talonid. Wasatch beds. *U. massetericus* Cope. Bridger beds. *U. vorax* Leidy.

Miocyon (*Prodaphaenus*) Wortman and Matthew. M large, P_1 reduced. Uinta beds. *M. scotti* Wortman and Matthew.

Vassacyon Matthew. *M* with pitted talonid, *P* small. Mandible high. Wasatch beds. *V. promicrodon* Wortman and Matthew.

According to Matthew, the three following named genera resemble the *Cercoleptidae*. They have the carnassials but little differentiated, and the molars are uniform.

Oodectes Wortman. Lower molars with strongly developed trigonid and trenchant talonid. Upper molars with protoconule, but lacking hypocone. *P* short and high. Bridger beds. *O. herpestoides* Wortman.

Vulpavus Marsh. $\frac{4\text{-}3}{4\text{-}3}$ *P.* Lower molars with low three-pointed trigonid, and broad talonid. *P* large. Upper *M* with median tubercles and thickened inner cingulum. Wind River beds. *V. canavus* Cope. Bridger beds. *V. palustris* Marsh and *V.* (*Phloodectes*) *ovatus* Matthew.

Palaearctonyx Matthew. *P* reduced, *M* low, flattened, superiorly large and subquadrate in outline. Bridger beds. *P. meadi* Matthew.

Suborder B. FISSIPEDIA. Carnivora Vera.[1]

Digitigrade or plantigrade carnivores, some of which are likewise omnivorous; with large convoluted cerebrum. I $\frac{3}{3}$ rarely $\frac{2}{2}$, canines exceeding the other teeth in size. P trenchant, carnassials P^4 and M_1. Upper M and lower M_2 and M_3 tubercular, at times exceedingly blunted or disappearing. Digits separated, extremities penta- or tetradactyl, the pollex and hallux seldom reduced; scapho-lunar and centrale fused. Terminal phalanges with pointed, compressed, curved claws which are sometimes retractile but never bifid.

The *Fissipedia* or *Carnivora* in the restricted sense resemble the *Creodontia* very closely in general aspect, skeletal and cranial structure, and in dental characters. The skull in primitive types agrees with that of the creodonts in its depressed form and elongated jaws, but in the higher types the facial region becomes shortened and the profile steeper. The parietals develop a sharp sagittal crest, which usually divides anteriorly into two divergent branches. There is always a strong zygomatic arch, while the palate is completely ossified, the auditory bulla swollen. The brain cavity is large,

[1] *Cope, E. D.* Amer. Naturalist, 1880, p. 833.—*Ibid.*, 1883, p. 235.—*Filhol, H.* Archiv. Mus. Hist. Nat. Lyon, vol. iii., 1883.—*Flower, W. H.* Proc. Zool. Soc. London, 1869.—*Gaillard, Cl.* Archiv. Mus. Hist. Nat. Lyon, vol. vii., 1899.—*Lydekker, R.*, Siwalik and Narbada Carnivora. Palæontologia Indica, ser. 10, vol. ii., 1884.—*Mivart, St. G.* Proc. Zool. Soc. London, 1882, 1885.—*Teilhard, P.* Annales de Paléont., vol. ix., 1914–15.—*Winge, H.*, Jordfundne og nu levende Rovdyr (Carnivora) fra Lagoa Santa. E Museo Lundii, Kjøbenhavn, 1895.—*Wortman, J. L.*, and *Matthew, W. D.* Bull. Amer. Mus. Nat. Hist., N.Y., 1899, p. 103.

the strongly convoluted cerebral hemispheres covering the greater part of the cerebellum and olfactory lobes. It is noteworthy that the *Fissipedia* are differentiated from the *Miacidae* only through the anchylosis of the scaphoid and lunar, the complete ossification of the auditory bulla, and the greater development of the brain.

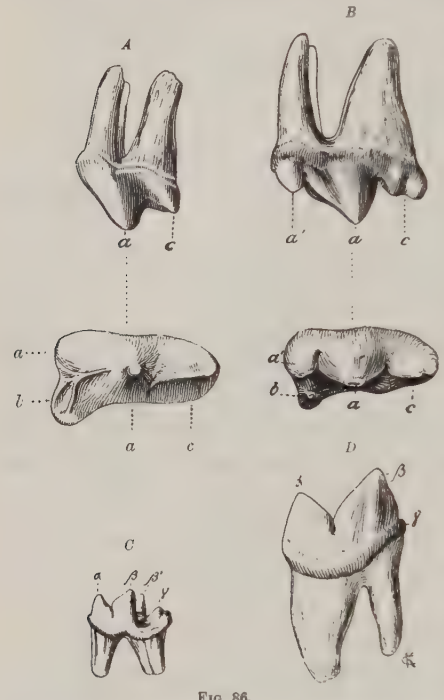


Fig. 86.

A, Lateral and superior aspect of upper carnassial of dog, and *B*, of lion. *C*, Lower carnassial of *Herpestes*, and *D*, of lion.

The large size of the canines, and the presence of shear-like carnassial teeth, are characters which stand in correlation with a carnivorous diet. The last premolar in the upper jaw, and the first molar in the lower are usually sectorial, resembling the *Miacidae*; the teeth in front of these have cutting edges, are tritubercular, and are often small and conical; those behind have broader crowns and are tuberculo-sectorial. The carnassial teeth are often, but not always, much larger and especially longer than the rest of the molar and premolar series.

The typical upper carnassial (Fig. 86) is three-rooted, consisting of a more or less compressed blade supported by two of the roots, the third bearing an inner tubercle. The blade, when fully developed, is trilobed, but the anterior cusp (*a'*) is always small, and sometimes absent. The middle cusp (*a*) is conical, high, and pointed, the posterior (*c*) has a compressed, trenchant edge, and is generally longer and lower than the anterior. The inner tubercle (*b*) varies in extent, and is generally anterior, though sometimes median, in position. In the *Ursidae* alone, both the inner tubercle and its supporting root are absent, and there is often a small internal and posterior cusp without a root. In the *Felidae*, *Hyaenidae*, and certain *Viverridae* there may be two small tubercles instead of one, anterior to the median cusp.

The lower carnassial is two-rooted and characterised by a strong development of the protoconid and paraconid, as against the stunted protocone and rudimentary paracone of the upper molars. The posterior lobe of the blade (β) is generally larger and higher than the anterior (α), and separated from it by a notch. In the *Felidae*, only the blade of the lower carnassial is developed, both talonid and inner cusp being absent or rudimentary. In some forms the talonid (γ) is greatly developed, broad and tuberculated, in which case the blade is generally placed obliquely. The inner cusp, when present, is generally conically pointed, and placed at the inner side of the blade.

All three upper molars may be present, or their number may be reduced

to one or two. In purely carnivorous forms, the crowns are broader than long, and trituberculate; while in omnivorous carnivores they are quadri- or multituberculate. The posterior molars degenerate or disappear as the diet becomes more exclusively carnivorous; on the other hand, in the frugivorous bears and *Mustelidae* the premolars exceed the carnassials in size. There may be one or two lower molars in addition to the carnassial, their crowns consisting of a bilobed anterior portion and a talonid. M_3 is often very small or may disappear.

In the milk dentition (Fig. 87), D_4 is essentially like M_1, and the lower carnassial D_3 like P_4. In the upper jaw, also, D^4 is, on the whole, similar structurally to M^1, and D^3 to P^4, and D^2 is very like P^3. All of the milk teeth are, however, slenderer than those of the mature dentition. D^4 has, as a rule, no inner basal cingulum, the lower D_4 has rather a large talonid, and the inner cusp of D^3 is placed more posteriorly than on P^4. The roots of all the deciduous molars are more widely divergent than those of the premolars.

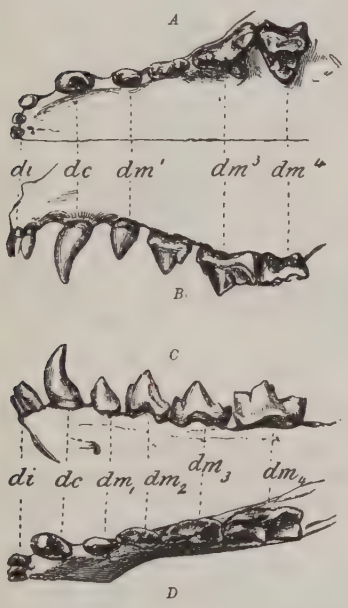


FIG. 87.

Milk dentition of *Viverra civetta* Linn. (After Mivart.) *A*, *B*, Inferior and lateral aspect of upper jaw. *C*, *D*, Lateral and superior aspect of lower jaw.

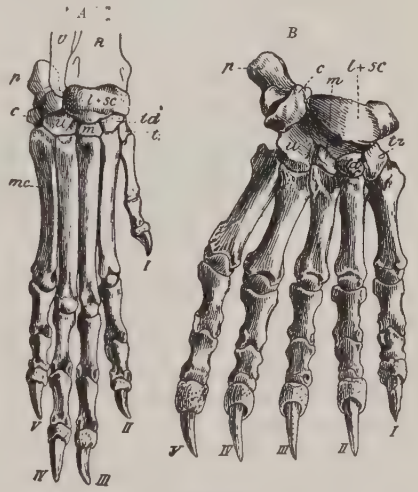


FIG. 88.

Manus, *A*, of dog and *B*, of bear. *R*, Radius; *U*, ulna; *l+sc*, scapho-lunar; *c*, cuneiform (triquetrum); *p*, pisiform; *u*, unciform; *m*, magnum; *td*, trapezoid; *tz*, trapezium; *mc*, metacarpals; *I.-V.*, first to fifth digits.

The pectoral girdle sometimes includes a rudimentary clavicle, and the humerus may possess an entepicondylar foramen. Radius and ulna remain distinct. Usually five digits are present, of which the first is generally much shorter than the others (Fig. 88). In the cats and civets, the pointed ungual phalanges are capable of retraction over the second phalanges. The femur always lacks a third trochanter. The tarsals are closely crowded, the fibula has an articular surface for the calcaneum,

the astragalus is deeply grooved superiorly and convex inferiorly, seldom completely truncated.

The Carnivora proper are divided into seven families: *Canidae*, *Ursidae*, *Procyonidae*, *Mustelidae*, *Viverridae*, *Hyaenidae*, and *Felidae*, all of which are represented in Tertiary and existing faunas.

Family 1. Canidae. Dogs.[1]

$\frac{3.1.4.3\text{-}2.}{3.1.4.3(4)\text{-}2.}$ *P^4 with moderate inner cusp, strongly developed primary cusps and long, shearing surface. P^3 and P_4, usually also P_3, with secondary cusps. Upper M tritubercular, broader than long and frequently with intermediate cusps. M_1 with high trigonid, moderately large metaconid and pitted, rarely trenchant talonid. M_2 flatter and smaller than M_1. Paroccipital process prominent and abutting on bulla. Extremities digitigrade, originally pentadactyl, later with pollex and hallux greatly reduced. Claws not retractile. Tail long. Os penis present.*

The *Canidae* (comprising the dogs, wolves, jackals, and foxes) have at present a cosmopolitan distribution. In external appearance as well as in dentition, they resemble the *Viverridae* most closely, although early differentiated from them as true *Miacidae* while in the Creodont stage. They first appear in the Upper Eocene of Europe, the *Amphicyoninae* alone being present in the Oligocene and Lower Miocene; later, they become more common in the Pliocene and Pleistocene. Their development is greatest in the Middle Tertiary of North America, from which they have become distributed to Europe through Asia, appearing also in South America.

Subfamily 1. Cynodictinae.

$\frac{2\text{-}3}{3}$ *M. P slender, with secondary cusps, upper M much wider than long, with intermediate cusps; lower carnassial with high and massive trigonid, basin-shaped talonid. Humerus with entepicondylar foramen. Extremities pentadactyl, semi-digitigrade. Metapodia with hemispherical, distal articular ends. Astragalus distally convex, claws partially retractile.*

The skeletal and dental characters most nearly resemble those of the *Viverridae*, the distinguishing feature being the presence of three molars.

Procynodictis Matthew and Wortman. Upper *M* lacking median tubercle. Uinta beds (Upper Eocene).

Protemnocyon Hatcher. *C* stout and compressed, *P* with lateral cusps. Upper molars with protoconule. M^3 reduced; lower molars with trenchant talonid. Brain cavity much inflated, sagittal crest very low; atlas resembling that of *Canis*. Supposed to be in the ancestral line of *Mesocyon*. White River beds (Oligocene).

[1] *Hatcher, J. B.*, Oligocene Canidae. Mem. Carnegie Mus., vol. i., 1902.—*Huxley, Th.*, Dental and cranial characters of the Canidae. Proc. Zool. Soc. London, 1880.—*Merriam, J. C.*, Pliocene and Quaternary Canidae. Univ. California Publ., 1903, 1913.—*Peterson, O. A.*, Description of new Carnivores from the Miocene. Mem. Carnegie Mus., vol. iv., 1910.—*Scott, W. B.*, Notes on the Canidae of the White River Oligocene. Trans. Amer. Philos. Soc., vol. xix., 1898.—*Studer, Theodor*, Die prähistorischen Hunde. Abhandl. Schweiz. Paläont. Ges., Bd. xxviii., 1901.—*Woldrich, J.*, Die Caniden aus dem Diluvium. Denkschr. Wien. Akad., math.-naturw. Kl., 1878; Bd. lxxxix.—*Wortman, J. L.*, and *Matthew, W. D.* Bull. Amer. Mus. Nat. Hist., New York, 1899.

Temnocyon Cope. Upper *M* triangular in outline, talonids of lower molars trenchant. John Day beds (Miocene); Oregon. *T. altigenis*, supposed ancestor of *Cyon*.

Mesocyon Scott (*Hypotemnodon* Eyermann). Talonid of M_1 trenchant, M_2 and M_3 basin-shaped. *M. coryphaeus* Cope sp. Same horizon and locality as the preceding.

Cynodictis Bravard and Pomel (Fig. 89). $\frac{2}{3}$ *M.* Upper molars very broad, triangular, with two rounded external cusps, and crescentic inner cusp. Lower carnassial with high external and strong internal cusps, talonid large. *C. lacustris* Gervais; *C. intermedius* Filhol. Gypsum beds of Paris; Débruge; also Quercy Phosphorites.

Galecynus Owen (*Cynodictis* Wortman). Upper molars triangular in outline, rounded; P^4 short. Oligocene. *G. paterculus* Matthew sp. *G. gregarius* Cope. White River beds. *G. oregonensis* Merriam sp. John Day beds. *G. oeningensis* von Meyer. Upper Miocene; Europe.

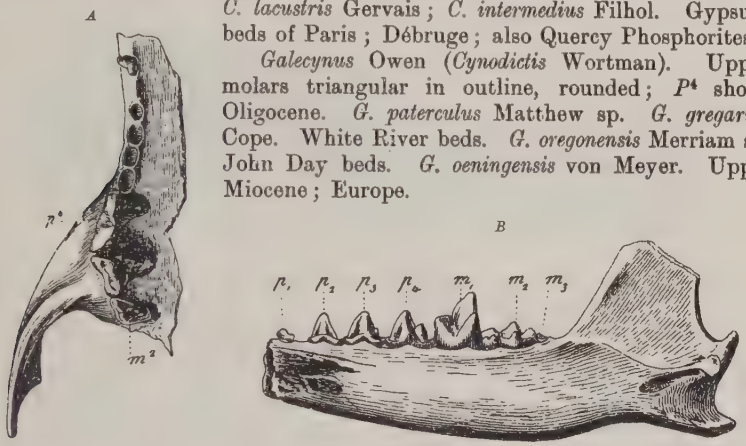


Fig. 89.

Cynodictis lacustris Gerv. Upper Eocene; Phosphorites of Quercy. *A*, Fragment of right upper jaw. *B*, Internal aspect of right mandible. $\frac{1}{1}$.

Nothocyon Matthew (*Galecynus* Cope). Upper molars large, upper carnassial small. Lower molars with well-developed hypoconid. *N. geismarianus* Cope sp., John Day beds. *N. annectens* Peterson, with larger carnassial, from the Lower Miocene of Nebraska, is regarded as ancestral to existing South American *Canidae*.

Cynodesmus Scott. *M* resembling those of *Lupus*, *P* with high cusps and secondary tubercles. Extremities pentadactyl, hallux abbreviated. *C. thooides* Scott. Miocene, Montana. *C. thomsoni* Matthew. South Dakota.

Philothrax Merriam. Jaw short and stout; premolars three in number. *P. condoni* Merriam. John Day beds, Oregon.

Subfamily 2. Amphicyoninae.

$\frac{3\text{-}2}{3\text{-}2}$ *M. Upper carnassials short and usually thickened, having an inner tubercle which may be either broadened anteriorly or displaced towards the median line; remaining P mostly small and simple.* M^1 *rounded, triangular, or quadrate in outline, with well-developed cingulum internally, generally also externally; with two anterior conules, and one, less often two, inner tubercles; median tubercles may be present.* M^2 *and* M^3 *oval.* M^3 *often wanting. Lower molars with small metaconid,*

and indented or cutting talonid. M^3 and M_3 frequently wanting. Humerus with entepicondylar foramen. Manus and pes pentadactyl, with proportionately short metapodia; claws somewhat retractile. Tail long.

In the later forms of the Upper Miocene and Pliocene of North America there is a shortening of the cranium which is correlated with the disappearance of M^3, the shortening of M_2 and M_3, and commonly with the reduction of the number of premolars. P^4 may become complicated, while M_2 may develop a long talonid when M_3 is lost.

FIG. 90.

Amphicyon giganteus Laurill. Miocene; Sansan (Gers). Inferior aspect of left upper jaw. $\frac{3}{5}$. (After Gaudry.)

Amphicyon Lartet (Fig. 90). $\frac{3}{3}$ *M.* M^3 always small; M^1 and M^2 tritubercular with V-shaped cusps; lower *M* slender, with weakly or strongly developed trenchant talonid. Numerous species varying in size between spaniels and bears. Quercy Phosphorites (Oligocene), *A. ambiguus* Filhol. Lower Miocene of Europe, *A. lemanensis* Pomel. Upper Miocene, *A. major* Blv. Lower Miocene of India, *A. shabazi* Pilgrim. Pliocene, *A. palaeindicus* Lydekker.

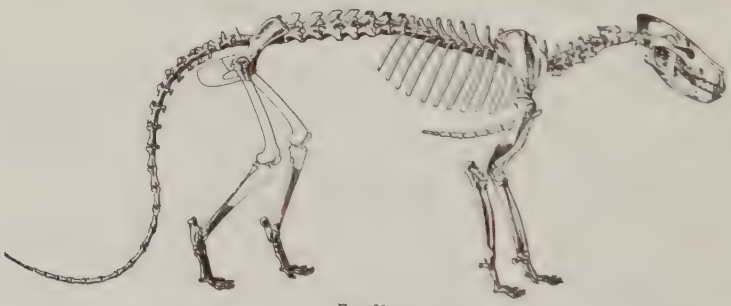


FIG. 91.

Daphaenodon superbus Peterson. L. Miocene; Sioux Co., Nebraska. Restored skeleton. $\frac{1}{15}$. (After Peterson.)

Reproduced, by permission, from The Memoirs of the Carnegie Museum.

Daphaenus Leidy. $\frac{3}{3}$ *M.* Somewhat resembling *Amphicyon*, and represented by perfect skeletons. White River beds (Oligocene). *D. felinus* Scott; *D. vetus* Leidy. *Daphaenodon* Peterson (Fig. 91). A later form and a successor to *Daphaenus*. Skeleton well known and larger than the preceding. *D. superbus* Peterson; Lower Miocene, Nebraska.

Paradaphaenus Matthew. John Day beds (Basal Miocene). *P. cuspiaerus* Cope sp.

Pseudamphicyon Schlosser. $\frac{2}{3}$ *M.* Lower P_4 and M_1 with prominent anterior cusps. Superior molars with weak cingulum. Metapodials very short, toes expanded. *P. lupinus* Schlosser. Eocene and Oligocene; Bohnerz.

Pseudocyon Lartet. $\frac{3}{3}$ *M.* Protocone of upper molars weak, talonid weak; cingulum strongly developed. Miocene; Tuchorschitz. *P. bohemicus* Schlosser. Sansan (Gers). *P. sansaniensis* Lartet.

Pseudarctos Schlosser. $\frac{3}{3}$ *M.* *P* and M_1 small; M_2 and M_3 large and flat. *P. bavaricus* Schlosser. Upper Miocene; Tutzing.

Simocyon Wagner. $\frac{2}{2}$ *M.* M_2 with long talonid; anterior *P* greatly reduced; skull abbreviated. Lower Pliocene; Pikermi and Eppelsheim.

Borophagus Cope (*Dinocyon* Matthew). $\frac{2}{3}$ *M.* Upper molars very broad, *P* weak. Cranium short and heavy. *B. gidleyi* Matthew. Miocene of Montana, Texas and Nebraska. "*Amphicyon*" *americanus* Wortman and *Borocyon robustum* Peterson possibly belong in this vicinity.

Ischyrocyon Matthew. $\frac{4}{4}$ *P.* First molar lacking internal cusp. Loup Fork beds; South Dakota.

Hyaenognathus Merriam. $\frac{4}{3}$ *P*, $\frac{2}{3}$ *M.* *P* $\frac{4}{4}$ large and stout in both jaws. Anterior *P* and posterior *M* very small. I^3 the size of *C*, inferior incisors contiguous. *H. pachyodon* Merriam. Pliocene of California. This form may be hyaenoid in nature.

Aelurodon Leidy (Fig. 92). $\frac{4}{4}$ *P*, $\frac{2}{3}$ *M.* *P*, with exception of last, small, but with lateral cusps. P^4 with large inner tubercle and strong cusp preceding paraconid. M_1 moderately long. Upper Miocene; Nebraska, S. Dakota and Kansas. *A. saevus* Leidy. *A. wheelerianus* Cope.

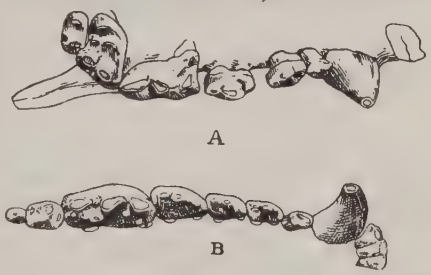


FIG. 92.

Aelurodon wheelerianus Cope. Miocene of South Dakota. *A*, Upper, and *B*, lower tooth-row. 1/2. (After Matthew.)

Enhydrocyon Cope (*Hyaenocyon* Cope). $\frac{2}{3}$ *P*, $\frac{2}{2}$ *M.* Cranium greatly shortened. P^4 lacking anterior tubercles. $M\frac{2}{2}$ very small. M_1 with trenchant talonid, and lacking metaconid. John Day beds (Lower Miocene). *E. stenocephalus* Cope. *E. crassidens* Matthew.

Subfamily 3. CYNODONTINAE.

Dentition $\frac{2\text{-}1}{3\text{-}2}$ *M.* *P^4 with large posteriorly displaced inner tubercle, remaining P small and simple. Upper M with moderate inner cingulum, large protocone and metaconule, and two outer conules; protoconules never present. M^1 not much shorter than broad, triangular; M^2 elliptical. Lower carnassial with weak metaconid, and generally with large indented talonid.*

The *Cynodontinae*, beginning with small forms, attain the size of bears in the Pliocene. Two lines of descent are observable: one represented by forms like *Cephalogale* and *Dinocyon*, possessing a dentition similar to that of the *Canidae*, and becoming extinct in the Pliocene; the other typified by *Cynodon*, and approximating the *Ursidae* in the enlargement of the molar teeth. The

first line of descent is characterised by a reduction of the premolars and molars, with a thickening of the teeth that remain. The *Cynodontinae* are mostly restricted to Europe.

Cephalogale Jourdan. $\frac{2}{3}$ *M.* M^1 rounded and triangular, M^2 diagonally oval. *P* smaller than *M*. Lower *M* with large trigonid and short, trenchant hypoconid; all with strong basal cingulum. Muzzle and jaws shortened, extremities slender, almost digitigrade; metapodia long, closely apposed. Upper Eocene, Bohnerzen of Switzerland and Swabia; Lower Miocene of St. Gérand le Puy and Mayence; Upper Miocene of Silesia.

Dinocyon Jourdan. $\frac{2}{3}$ *M.* Lower *M* usually with short, trenchant talonid; M^1 rounded, triangular; M^2 oval; P^4 large and complex. Astragalus flat. Upper Miocene and Lower Pliocene of Europe. Blanco beds (Pliocene) of Texas.

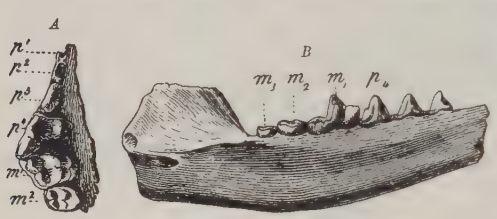


FIG. 93.

Cynodon leptorhynchus Filhol sp. Phosphorite of Mouillac, Quercy. *A*, Lower aspect of the right upper jaw. *B*, Inner aspect of the left lower jaw. $\frac{1}{1}$.

Hemicyon Lartet. P^4 with posteriorly placed tubercle, *M* as in *Cephalogale*. Extremities digitigrade. Upper Miocene, Sansan.

Cynodon Aymard (Fig. 93). P^4 with large inner tubercle, first three *P* small. Upper *M* quadrangular, but little broader than long. Metacone and protocone subequal. Talonid of lower *M* moderately large, basin-shaped. Digits laterally extended. *C. leptorhynchus* Filhol sp.; *C. velaunus* Aymard. Oligocene of Ronzon, Quercy and Ulm.

Paracynodon Schlosser. *M* with wrinkled enamel. *P. vulpinus* Schlosser. Oligocene; Bohnerz of Ulm.

Pachycynodon Schlosser. Mandible very high. *P* small. Upper carnassial with large posteriorly extending inner cusp. Upper *M* quadrangular, lower *M* with large basin-shaped talonid. *P. crassirostris* Filhol sp. Quercy Phosphorites (Oligocene), Bohnerz of Swabia.

Subfamily 4. CANINAE.

$\frac{2}{3\text{-}2}$ *M. P slender, posteriors with secondary cusps. Upper M tritubercular with strong cingulum, lower carnassial with weak metaconid, and others usually with pitted or trenchant talonid. Humerus lacking entepicondylar foramen. Extremities digitigrade, tetradactyl, with rudimentary hallux and pollex. Metapodials with cylindrical distal articular surfaces; astragalus distinctly truncate.*

Canis Linn. $\frac{2}{3}$ *M.* Talonid partly trenchant, with small or rudimentary entoconid. A large number of extinct species is known, among which are *C.* (*Tephrocyon*) *temerarius* Leidy from the Upper Miocene of North America; *C. cautleyi* Bose, in the Siwalik Pliocene of India, probably also in China; *C. etruscus* Major, in the Upper Pliocene of Tuscany; *C. lupus* Linn. in the Pleistocene of Europe; *C. latrans* Say, *C. indianensis* Leidy, *C. occidentalis* Rich, in the Pleistocene of North America. In the European Pleistocene there were the

wild dogs, *C. mikii*, *C. intermedius*, and *C. hercynicus*. The dingo occurs fossil in Australia. The domestic species, *C. familiaris*, first appears during the Neolithic period. Remains of the marsh dog, *C. familiaris palustris*, and of the large *C. familiaris inostranzewi*, are found in the Swiss lake dwellings.

Other varieties (*C. familiaris matris optimae* and *C. leineri*) occur in the Bronze Age. According to Studer, it is probable that the innumerable varieties of existing domestic dogs have a common ancestor. Originally descended from one or more Pleistocene species of wolf-like wild dogs, their manifold subsequent modifications have been all brought about by breeding, as well as to some extent also by crossing with wolves and jackals. The dogs of the southern hemisphere have probably sprung from a dingo-like ancestor.

Vulpes Brisson. Talonid of lower *M* basin-shaped. *C* and *M* slender. *V. vulgaris* Linn. sp. occurs fossil in the Pleistocene of Europe; *V. donnizani* Depéret in the Middle Pliocene of Roussillon; *V. borbonicus* Brav. and *V. megamastoides* Pomel in the Pliocene of Auvergne; *V. alopecoides* Del Campana in the Pliocene of Val d'Arno. *V. sinensis* Schlosser in the Pliocene of China, and *V. curvipalatus* Bose in the Indian Siwalik. The oldest fossil representative of the genus *Vulpes* is probably *C. vafer* Leidy, in the Upper Miocene of North America.

Leucocyon Pallas. The arctic fox (*Leucocyon lagopus* Pallas) is common with the reindeer and lemming in the European Pleistocene.

Cyon Blanford. Dentition usually $\frac{2}{2}$ *M*. Lower molars with trenchant talonid. Recent in Asia, fossil in European Pleistocene.

Icticyon and *Palaeocyon* Lund. Fossil in Brazilian bone caverns.

Otocyon Lichtenstein. $\frac{3}{4}$ *M*. One recent species from South Africa.

Family 2. Ursidae. Bears.[1]

$\frac{3.1.4\text{-}1.2.}{3.1.4\text{-}1.3.}$. *C robust, large; P always small in comparison with the molars. P_2 and P_3, less frequently P_1, lacking. P $\frac{4}{4}$ short, P^4 with two blunted outer tubercles, and a posteriorly broadened, but displaced, inner tubercle. Upper molars more or less quadritubercular, much longer than broad. M_1 with low trigonid, M_2 and M_1 with large concave talonid, rarely trenchant; M_3 with rounded crown. Cranium elongated, auditory bulla flattened. Paroccipital and mastoid processes strongly developed. Extremities large, pentadactyl and plantigrade, fifth digit larger and stronger than the others. Tail short, os penis large.*

The bears comprise large, mostly omnivorous carnivores, distinguished as to dentition by the absence of true carnassials, and the presence of typically quadrate, or subquadrate, multitubercular molars. In skeletal features they resemble the *Amphicyoninae*, but are more stoutly and compactly constructed. The plantigrade extremities are adapted for climbing and grasping. Bears are recent and fossil in Europe, Asia, North Africa, North and South America. In America they appear first in the Pliocene, originating first in Europe as an offshoot of the *Cynodontinae*, which in turn are derived from a *Miacidean* stock.

Hyaenarctos Falconer and Cautley (Fig. 94). Anterior *P* small, deciduous; superior *M* quadritubercular, quadrate, with wrinkled enamel and of uniform

[1] *Merriam, J. C.*, An American Pliocene Bear. Univ. Calif. Publ., Geol., 1916.—*Schlosser, M.*, Die Bären des europäischen Tertiärs. Paläontogr. Bd. xlvi., 1899.—Parailurus und Ursus aus den Ligniten von Baroth. Mitteil. Jahrb. k. Ungar. Geolog. Anstalt, Budapest, 1899.

size. Pliocene of Montpellier, Alcoy, Pikermi and the Indian Siwalik. *H. sivalensis*, *H. punjabiensis* Falc.; the latter in the Maragha beds also. One species in the Pleistocene of China. Also in Pliocene of North America.

Ursavus Schlosser. *P* small. P^4 with large inner tubercle, lower *M* with weak corrugations. Attains the size of a wolf. *U. brevirhinus* Hofmann sp., Upper Miocene of Styria and Silesia. *U. primaevus* Gaillard sp.; La Grive St. Alban and Pliocene Bohnerz of Swabia.

Ursus Linn. Upper *M* much longer than carnassial, corrugated, multitubercular, increasing in size from the first onwards. P^1 very much reduced, deciduous, often missing, and separated from the third by a wide diastema. The earliest fossil indications of this genus are in the Lower Pliocene of the Siwalik hills and China (*U. theobaldi* Lyd.). *U. boeckhi* Schlosser

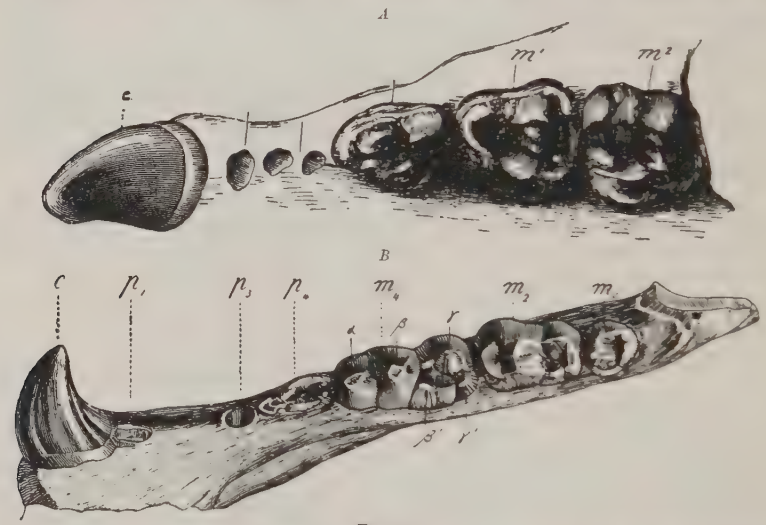


FIG. 94.

A, *Hyaenarctos sivalensis* Falc. Lower Pliocene of Siwalik Hills, India. Lower aspect of the left upper jaw. 3/5. (After Gaudry.) *B*. *Hyaenarctos punjabiensis* Lyd. Right half of the lower jaw. 3/5. (After Lydekker.)

occurs in the Pliocene of Transylvania; *U. etruscus* Cuv. in the Pliocene of Tuscany; *U. arvernensis* Croiz. in the Pliocene of Roussillon and Auvergne. The cave bear (*U. spelaeus* Blumenb.) is the most abundant carnivore of the European Pleistocene, the various caverns having yielded more than 100 skeletons in various states of preservation. This species is distinguished from the existing brown bear (*Ursus arctos*) by its larger size, more robust bones, more convex brow, and the absence of P^1. Its ancestor was *U. deningeri* Reichenau in the early Pleistocene. *U. priscus* Cuv., from the European Pleistocene, is closely related to the grizzly bear. Other Pleistocene species occurring in North America are *U. americanus* Pallas, *amplidens* Leidy, *vitabilis* Gidley, and *floridanus* Merriam.

Arctodus Leidy (*Arctotherium* Bravard). Jaws greatly shortened, *P* crowded. In the Pleistocene of California and South Carolina. *A. pristinus* Leidy; *A. simus* Cope sp. in Pennsylvania; Mexico, and South America, *A. bonariensis* Gervais sp.

Family 3. **Procyonidae** (*Subursi* Blainville). Raccoons.

$\frac{3.1.4\text{-}3.2.}{3.1.4\text{-}3.2\text{-}3.}$. *No typical carnassials. Upper molars and last premolar rounded, quadrate, tritubercular or quadritubercular. Lower M with blunted trigonid, and bitubercular talonid. Cranium short and broad. Extremities pentadactyl, plantigrade.*

The *Procyonidae* are, with the exception of the isolated Himalayan genus *Ailurus*, recent forms of the American region. They may have been derived from the *Miacidae* or, according to Teilhard, from the *Cynodontinae* (*Pachycynodon*).

Procyon Storr. Raccoon. Recent and in the Pleistocene of North and South America.

Bassariscus Coues. Recent and in the Pleistocene and Pliocene of North America. *B. antiquus* Matthew.

Nasua Storr. Recent and fossil in Pleistocene of South America.

Cyonasua and *Pachynasua* Ameghino are found in the Parana beds; *Amphinasua* Moreno in the Araucanian strata of the Argentine Pliocene.

Phlaocyon Matthew (Fig. 95). $\frac{4\ P,\ 2\ M}{4\ P,\ 3\ M}$. Cranium and skeleton resembling that of *Procyon*. Teeth resembling those of *Cynodictis*, but last premolar more complex, possessing two inner tubercles. Large auditory bullae. *P. leucosteus* Matthew. Lower Miocene of Colorado.

Fig. 95.

Phlaocyon leucosteus Matthew. Miocene of Colorado. Lower aspect of the skull. $^1/_2$. (After Matthew.)

Leptarctus Leidy. $\frac{\quad}{3.1.3.2}$. *P* with talonid,

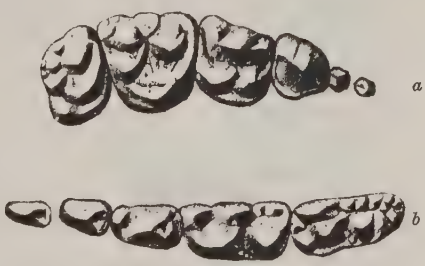


Fig. 96.

Parailurus anglicus Boyd Dawkins sp. Pliocene of Baroth, Transylvania. *a*, Upper, and *b*, lower tooth-row, P_2-M_2. $^1/_1$.

mandible high and truncate in front. Related to *Procyon*. Loup Fork beds, South Dakota.

Parailurus Schlosser (Fig. 96). *M* highly complicated; *P* much simpler than in the living genus *Ailurus*. Red Crag of England and Pliocene Lignite of Baroth, Transylvania.

Cynarctus Matthew. Three molars in lower jaw. M_1 with cusp toward outer side of protoconid, M_2 also with protoconid. Coronoid process of mandible triangular. *C. saxatilis* Matthew. Regarded by Matthew as belonging to the *Canidae*. Loup Fork beds, Colorado; Upper Miocene.

Family 4. Mustelidae.

$\frac{3.1.4.2\text{-}1.}{3.1.4.2.}$ *Upper carnassial* P^4 *with long blade behind anterior cusp, and with strong inner cusp. Lower carnassial* M_1 *with well-developed, grooved or trenchant talonid, usually with small metaconid.* M^1 *transversely broadened, frequently large and quadrangular, usually with well-defined cingulum.* M^2 *if present, very small;* M_2 *greatly reduced, but often two-rooted. Auditory bulla lacking septum, convex, usually small, distinct from paroccipital process. Alisphenoid canal wanting. Body elongated, feet mostly pentadactyl, planiigrade or digitigrade.*

The *Mustelidae* are small to moderately sized, slender, active carnivores existing principally in the northern hemisphere, but, with the exception of Australia, world-wide in distribution. Fossil forms are similarly distributed. The basicranium exhibits great similarity to that of the *Ursidae*. In the earliest fossil forms, the auditory bulla is strongly convex, while the dental formula is $\frac{2}{2\text{-}3}$ *M*, and they are not markedly differentiated from the earliest *Viverridae*, from which they are probably descended.

Subfamily 1. Putoriinae.

$\frac{2}{2}$ *M, later becoming* $\frac{1}{2}$ *M. Marked reduction of* $P\ \frac{4}{4}$, M^2, *metaconid of* M_1, *as well as the small talonid of* M_1.

Palaeoprionodon Filhol. $\frac{2}{2}$ *M*. Upper *M* tritubercular, M_1 with metaconid, and small indented talonid; M_2 small and two-rooted. Quercy Phosphorites (Oligocene).

Stenoplesictis Filhol (Fig. 97). Quercy Phosphorites (Oligocene).

Bunaelurus Cope (Fig. 98). *B. lagophagus* Cope. Cranium well known. White River beds; Colorado.

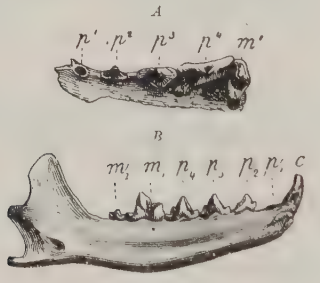


Fig. 97.

Stenoplesictis cayluxi Filhol. Phosphorites of Quercy. *A*, Lower aspect of the left upper jaw. *B*, Inner aspect of the left mandible. 1/1.

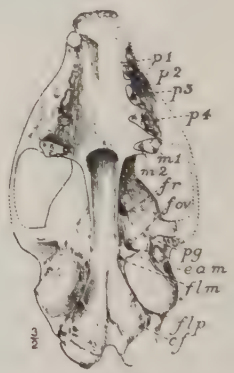


Fig. 98.

Bunaelurus lagophagus Cope. Oligocene White River beds, Colorado. Lower aspect of skull. 1/1. (After Matthew.)

Paractis Scott. John Day beds (basal Miocene).

Proailurus Filhol (*Haplogale* Schlosser). $\frac{1}{2}$ *M*. *M* with very short talonid and small metaconid. M_2 single-rooted. Phosphorites (Oligocene) to Upper Miocene.

Proputorius Filhol. Upper Miocene; Sansan.

Stenogale Schlosser. M_1 with metaconid, M_2 trenchant, single-rooted. Oligocene to Upper Miocene.

Pseudictis Schlosser. M_2 two-rooted. Upper Miocene, Günzburg.

Palaeogale von Meyer. M_1 lacking metaconid, M_2 two-rooted. Oligocene to Upper Miocene.

Putorius Cuv. Weasel. M_1 lacking metaconid, M_2 single-rooted. Pliocene of Auvergne and Recent.

Gulo Storr. Glutton. $\frac{4\text{-}1.}{4\text{-}2.}$ *P* and *M* thickened, M^1 bicuspid, M_1 lacking metaconid. Recent forms are circumpolar in distribution. Fossil in Pleistocene of Europe and North America.

Subfamily 2. MARTINAE. Martens.

M_1 constantly with inner cusp, and pitted talonid. M^1 small, P^4 with very small inner cusp.

Plesictis Pomel (Fig. 99). Dentition $\frac{2}{2}$ *M*. M^1 tritubercular. M^2 small or lacking, M_2 two-rooted. Phosphorites (Oligocene), Lower Miocene of Allier, Ulm, Mayence. Also Upper Miocene, Styria, and La Grive St. Alban.

Mustela Linn. $\frac{1}{2}$ *M*. M_2 single-rooted. Upper Miocene of Sansan, La Grive St. Alban and Styria; Pliocene of Pikermi, Bessarabia and Siwalik; also Pleistocene of Europe. *M. ogygia* Matthew. Miocene; N. America. *M. minor* Douglass. Pliocene; N. America.

Galictis Bell. Recent in South America. Fossil in Pleistocene of Brazil and Maryland.

Oligobunis Cope. $\frac{4\text{-}3}{4}$ *P*, $\frac{2\text{-}1}{2}$ *M*. About the size of a badger. Lower Miocene. *O. crassivultis* Cope. John Day beds. *O. lepidus* Matthew. Dakota.

Paroligobunis Peterson. 4 *P*, 2 *M*. Metaconid small, talonid trenchant. *P. simplicidens* Peterson. Lower Miocene; Nebraska. *P. lacota* Matthew and Gidley. Lower Miocene; Dakota.

FIG. 99.

Plesictis lemanensis Pomel. Lower Miocene of St. Gérand-le-Puy, Allier. Lower aspect of the skull. 3/4. (After Filhol.)

Aelurocyon Peterson. $\frac{4}{4}$ *P*, $\frac{2}{2}$ *M*. *Megalictis* Matthew. $\frac{?3}{?3}$ *P*, $\frac{2}{2}$ *M* are large forms with shortened cranium and muzzle. M_1 lacking metaconid, M_2 diminutive. *A. brevifacies* Peterson. Miocene; Nebraska. *M. ferox* Matthew. South Dakota; Miocene.

Subfamily 3. LUTRINAE. Otters.

Moderate-sized aquatic forms. M with metaconid and trenchant talonid. P^4 with broad inner tubercle.

Plesiocyon Schlosser. $\frac{2}{3}$ *M*. Quercy Phosphorites (Oligocene).

Amphictis Pomel. $\frac{2}{2}$ *M*. M_2 with long talonid. Quercy Phosphorites and Miocene. Referable to *Cynodontinae*, according to Teilhard.

Potamotherium Geoffroy (*Lutrictis* Pomel; *Stephanodon* v. Meyer) (Fig. 100). $\frac{4.2.}{4.2.}$ Upper carnassial with broadened inner cusp. M^1 transversely elongated, tritubercular. M^2 very small; M_1 with large talonid. Auditory bulla flattened. Skeleton more highly specialised than that of *Lutra*. Metapodials and toes flattened. Miocene of Dépt. Allier, Mayence and Ulm. Also in the Miocene of North America. *P. lycopotamicum* Cope, *P. lacota* Matthew. These are all well-distinguished forms.

Lutra Erxleben. Otter. $\frac{1}{2}$ *M*. *M* more compressed than in preceding genus. Recent in northern hemisphere and fossil in the Miocene, Pliocene and Pleistocene of Europe, N. Africa (Egypt), Asia and North America.

Brachypsalis Cope. M_1 very long. Miocene of Nebraska.

Enhydriodon Falconer. Basal Pliocene, Monte Bamboli; and Pliocene of Siwalik.

Fig. 100.

Potamotherium valetoni Geoffroy St. Hilaire. Lower Miocene of St. Gérand-le-Puy. Lower aspect of the skull. $\frac{2}{3}$.

Fig. 101.

Promeles palaeattica Weithofer sp. Lower Pliocene of Pikermi near Athens. *A*, Palate from below. *B*, Lower jaw from above. $\frac{1}{1}$. (After Weithofer.)

Subfamily 4. Melinae. Badgers.

M $\frac{1}{2}$. *M_1 with large grooved talonid, usually with metaconid. M^1 enlarged and complicated. Anterior P strongly reduced.*

Trochictis v. Meyer. M_1 with short talonid. Upper Miocene of Europe.

Trochotherium Fraas. *M* flattened. Upper Miocene; Germany.

Promeles Zittel (Fig. 101). $\frac{3.1.}{3.2.}$ P^4 elongated, M^1 tritubercular, quadrangular in outline, with well-developed cingulum. M_1 with long, multituberculate talonid. Basal Pliocene; Pikermi.

Meles Storr. Badger. P^4 short. Recent in Europe and Asia. Fossil in Lower Pliocene of Maragha (Persia) and China, and Pleistocene of Europe.

Taxidea Waterhouse. Recent, Pliocene and Pleistocene of North America.
Mellivora Storr. Recent in South Asia and South East Africa. Fossil in Pliocene of Siwalik.
Trocharion Major. M_2 two-rooted. Upper Miocene; La Grive St. Alban.
Promephitis Gaudry. P reduced to only $\frac{2}{2}$. Lower Pliocene; Pikermi.
Mephitis Cuv. $\frac{3}{3}$ *P.* Recent and fossil in Pleistocene of North America.
Thiosmus Illiger. South America.
Brachypotoma Brown. $\frac{2}{3}$ *I.* Pleistocene of North America.

Family 5. **Viverridae.** Civet Cats.

$\frac{3.1.4.2.}{3.1.4.2.}$ *Upper carnassial elongated, with anterior cusp preceding the principal cusp, and strong anterior inner tubercles far forward. Upper M tritubercular.* M_1 *with high, trilobate, trigonid and concave tubercular, talonid.* $M\frac{2}{2}$ *and* $M\frac{1}{1}$ *similar. Cranium elongated, low with moderately elongated snout. Tympanic bulla large and separated from the tympanic by a septum. Extremities short and slender, plantigrade or digitigrade, pentadactyl, occasionally tetradactyl. Tail long.*

The *Viverridae* are mostly small, slender and agile carnivores, existing at the present time exclusively in Asia, Africa and South Europe. They are represented by fossil remains in the European Tertiary, and in the Pliocene and Pleistocene of South Asia, being probably derived from the *Viverravinae* of the North American and European Eocene. In skeletal and dental structures they exhibit many characteristics of the oldest *Cynodictinae* and *Mustelidae* (*Palaeoprionodon*).

Viverra Linn. (Fig. 102) and *Herpestes* Illiger (Fig. 103) are recent in South

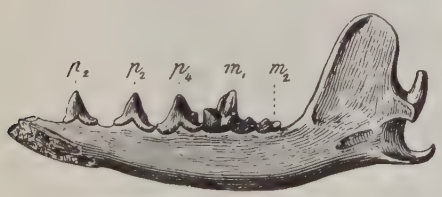


Fig. 102.
Viverra simplicidens Schloss. Phosphorite of Quercy. Inner aspect of right mandible. $\frac{1}{1}$.

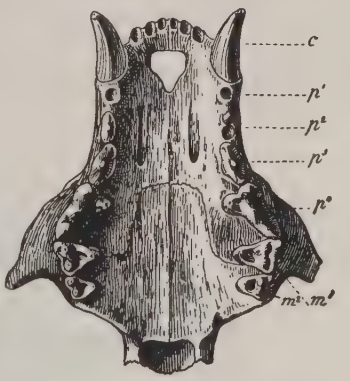


Fig. 103.
Herpestes lemanensis Pomel (*Viverra antiqua* Blainv.). Lower Miocene of Tretaux, Allier. Lower aspect of palate. $\frac{1}{1}$.

Asia, South Europe and North Africa. Fossil forms with small talonid and small M_2 in Quercy and English Eocene. From these, the various fossil species of *Viverra* and *Herpestes*, characteristic of the European basal Miocene, have been derived. *Progenetta incerta* Lartet appears first in the Upper Miocene and Pliocene of South France. *Viverra pepratxi* Depéret is known from Roussillon, and many typical species of *Viverridae* appear in the Siwalik beds.

Ictitherium Wagner (*Thalassictis* Nordmann, *Palhyaena*, Gervais) (Fig. 104). Cranium elongated, narrow; M^1 and M^2 small proportionately to P^4. Lower

Pliocene; Pikermi, Samos, Maragha, Lébéron, Bessarabia, China and India.

Fig. 104.

Ictitherium robustum Nordm. sp. Lower Pliocene of Pikermi near Athens. Lower aspect of the left upper jaw. $^1/_1$. (After Gaudry.)

Family 6. **Hyaenidae.** Hyaenas.

$\frac{3.1.4\text{-}3.1.}{3.1.4\text{-}3.1\text{-}2.}$ *Upper carnassial P^4 greatly elongated and strongly developed, with anterior cusp and posteriorly a long shearing blade. Anterior premolar small. Posterior Ps and canines robust, and cone-shaped. Lower carnassial M_1 with two long blades and faint talonid, rarely with metaconid. Tympanic bulla lacking septum. Fore-limbs longer than hind-limbs. Extremities digitigrade, manus and pes always tetradactyl. Second metacarpal overlapping the third. Os penis weak.*

The dentition of the *Hyaenidae* is characterised by a reduction of M^1, M_2, and the talonid and metaconid of M_1, the paraconid and protoconid becoming

Fig. 105.

Hyaena eximia Roth and Wagn. Lower Pliocene of Pikermi near Athens. $^1/_3$. (After Gaudry.)

transformed into a strong shear. The premolars, with the exception of those most anterior, become thick cones, the dentition being thus excellently adapted for the crushing of bones.

Ictitherium seems to be transitional between the *Hyaenoids* and the *Viverridae*. The *Hyaenidae* are recent in Africa and West Asia, and the

earliest fossil forms appear in the Pliocene of Europe and Asia. Certain *Canidae* of the North American Miocene, *Aelurodon*, *Hyaenognathus*, exhibit great similarity in dentition to the *Hyaenidae*.

Lycyaena Hensel (*Agnotherium*, *Agnocyon* Kaup) and *Hyaenictis* Gaudry, are distinguished from *Hyaena* by the more slender teeth and the presence of a small M_2. Basal Pliocene; Pikermi, Eppelsheim, Baltavár, and Bessarabia.

Hyaena Linn. (Fig. 105) appears first in Lower Pliocene of Pikermi, Samos, Maragha, Baltavár, Mont Lébéron, Bessarabia. *H. exima* Roth and Wagner; *H. salonicae* Andrews (Salonika). *H. colvini*, *H. macrostoma* Lydekker, *H. felina*, *H. sivalensis* Bose, in the Pliocene of Siwalik. *H. gigantea* Schlosser, in China. *H. arvernensis* Croiz. & Job., in the Upper Pliocene of Auvergne and valley of Arno. In Roussillon and Pleistocene of Mosbach, *H. perrieri* Croiz. & Job. and *H. brevirostris* Aym. In later Pleistocene of South Europe *H. striata*, resembling *H. arvernensis*; *H. crocuta* var. *spelaea* Goldf. in early European Pleistocene, greatly resembling *H. perrieri*. Found also in the Karnul Caves of India and in the Pleistocene of China, *H. sinensis* Owen.

Family 7. **Felidae.** Cats.[1]

$\frac{3.1.3\text{-}2.1.}{3.1.3\text{-}1.1(2).}$ *C strongly developed, antero-posterior borders sharpened. Upper carnassial elongated, trenchant, with inner tubercle and three outer cusps. Lower carnassial with two converging blades, developed from paraconid and protoconid, rudimentary talonid, unusually with weak metaconid.* M^1 *and* M_2 *always small. Number of premolars constantly reduced, the remaining premolars being provided with lateral cusps. Auditory bulla well rounded, septate, and lacking prolonged external meatus. Cranium inflated, muzzle short. Humerus with entepicondylar foramen. Extremities long and slender, digitigrade. Manus pentadactyl, pes more often tetradactyl. Claws retractile. Os penis small.*

The *Felidae* are universally distributed except in Australia and New Zealand, both at the present day and as fossils; they first appear in Europe and almost simultaneously in North America. They possess a reduced but at the same time highly specialised dentition, adapted for the cutting of flesh, while the skeleton combines the greatest strength with the utmost grace of form.

They are sharply differentiated from the other carnivores, and even their most remote ancestor yields no satisfactory information concerning their origin, all possessing the same typical characteristics. If the Miocene genus *Proailurus*, which Filhol regards on account of its similarity with the recent *Cryptoprocta* as ancestor of the *Felidae*, is really a member of this family, it is undoubtedly the ancestor of the true cats, but not of the *Machairodontinae*, since these are already present in the Oligocene or even the Upper Eocene. A possible derivation of both Felines and Machairodonts may be from *Dinictis*, according to Matthew. *Hoplophoneus* from the same formation as the latter is certainly more in line with the Machairodonts.

Subfamily 1. Machairodontinae.

Carnassial slightly notched. Inner cusp of P small. Upper C sabre-like, becoming gradually larger, lower C gradually smaller. P^3 *small,* P_2 *rudimentary or wanting.*

[1] *Fabrini, E. I.*, Machairodus di Valdarno. Boll. Comit. Geol. Roma, 1890.—*Matthew, W. D.*, The Phylogeny of the Felidae. Bull. Amer. Mus. Nat. Hist., 1910.

Occipital high and narrow projecting mastoid process, which becomes larger. Upper canine protected by a downward flange of the mandible. Extremities robust, hallux and pollex strong, digits expanding.

Eusmilus Gervais. $\frac{3.1.2.1.}{2.1.1.1.}$. M_1 lacking talonid and metaconid. Flanges of mandibular symphysis pendulous. *E. bidentatus* Filhol. Quercy Phosphorites. *E. dacotensis* Hatcher. Upper Oligocene; Dakota.

Hoplophoneus Cope (*Pogonodon* Merriam). Dentition $\frac{3.1.3\text{-}2.1.}{3\text{-}2.1.3\text{-}2.1.}$. M_1 without metaconid. $P\ \frac{2}{2}$ and $P\ \frac{3}{3}$ small, P_2 generally wanting, upper C slender. Auditory bulla incompletely ossified. White River beds (Oligocene). *H. occidentalis* Leidy.

Machairodus Kaup. $\frac{3.1.2\text{-}1.1.}{3.1.2.1.}$. P^4 usually with four external cusps. M_1 lacking metaconid and usually talonid. $P\ \frac{3}{3}$ rudimentary. C long, notched posteriorly. Mandibular flanges large. Bulla completely ossified. *M. palmidens* Blv., La Grive St. Alban. *M. jourdani* Filhol. *M. aphanistus* Kaup. Lower Pliocene of Pikermi, Veles, Eppelsheim and Samos. *M. orientalis* Macquenem. Maragha. *M. horribilis* Schlosser. China. *M. sivalensis* Lyd. Siwalik. *M. cultridens* Cuv. *M. crenatidens* Fabrini. Upper and Middle Pliocene of Europe. *M. latidens* Owen. European Pleistocene.

Smilodon Lund (*Trucifelis* Leidy; *Dinobastis* Cope; *Smilodontopsis* Brown). $\frac{3.1.2.1.}{3\text{-}2.1.2\text{-}1.1.}$. Upper carnassial usually with only three outer cusps. M_1 lacking talonid and metaconid. P^3 small, P_3 generally lacking. Hallux strongly developed. Restricted to the American continents. In the Pleistocene of North America. *S. gracilis* Cope; *S. floridanus* Leidy; *S. californicus* Matthew. In South America, *S. neogaeus* Lund.

Subfamily 2. Felinae.

Carnassials deeply notched. Upper carnassial with strong inner cusp. Upper C becoming smaller by degrees; lower C becoming larger. P^3 large, P_3 and P_4 of like strength. Mastoid process reduced, coronoid process enlarged. Hallux reduced. Extremities elongated, digitigrade.

Aelurictis Trouessart (*Aelurogale* Filhol). $\frac{3}{3}\ P,\ \frac{1}{2}\ M.$ M_2 weak, M_1 lacking metaconid, with strong talonid. Symphysis with acute border. Large metapodials. Quercy Phosphorites. *A. intermedia*, *A. minor* Filhol.

Dinictis Leidy (*Daptophilus* Cope) (Fig. 106). $\frac{3}{3}\ P,\ \frac{1}{2}\ M.$ In some cases there are four inferior premolars. M^2 occasionally present. M_1 with talonid and metaconid. C long, feebly serrated posteriorly. Mandibular symphysis with pendulous flanges. Carotid foramen distinct from foramen lacerum posterius. Auditory bulla incompletely ossified. Hallux functional. Metapodials short. *D. felina* Leidy. *D. squalidens* Cope. White River beds (Oligocene), North America. *D. cyclops* Cope. John Day beds (Lower Miocene); Oregon.

Nimravus Cope (*Archaelus*, *Pogonodon* Cope). Dentition $\frac{4\text{-}3}{3\text{-}2}\ P,\ \frac{1}{1\text{-}2}\ M.$ Greatly resembling *Aelurictis*. M_1 lacking metaconid, C moderately developed.

Symphysis lacking flange. *N. debilis, platycopis, gomphodus* Cope. John Day beds (Lower Miocene); Oregon. *N. sectator* Matthew. South Dakota.

Pseudaelurus Gervais (Fig. 107). $\frac{3}{3\text{-}2}$ *P*, $\frac{1}{1}$ *M*. M_1 lacking metaconid, but

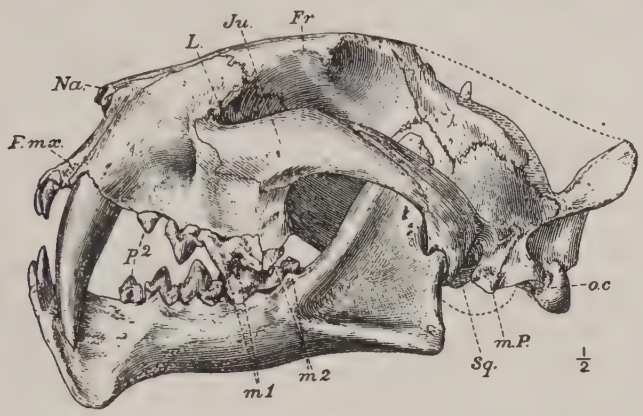


Fig. 106.

Dinictis felina Leidy. Oligocene of White River beds. Skull and lower jaw. 1/2. (After Matthew.)

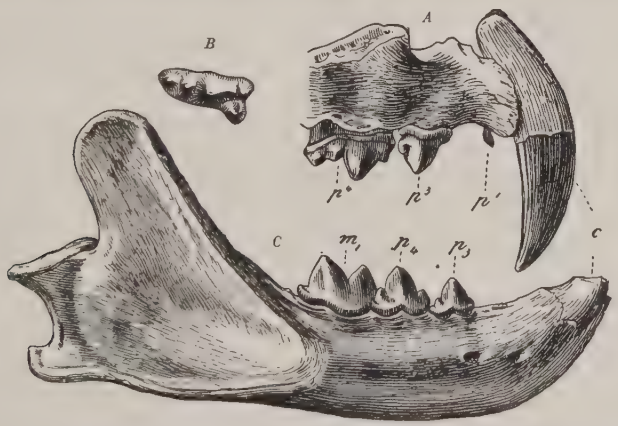


Fig. 107.

Pseudaelurus quadridentatus Blv. (*Felis hyaenoides* Lartet.) Miocene of Sansan, Gers. *A*, Fragment of the right upper jaw. *B*, Lower aspect of upper molar. *C*, Exterior aspect of right lower jaw. 2/3. (After Filhol.)

with small talonid. *C* normal. Symphysis lacking flanges. Upper Miocene. *P. quadridentatus* Blv. Sansan. *P. lorteti* Gaillard. La Grive St. Alban.

Felis Linn. $\frac{2\text{-}3}{2}$ *P*, $\frac{1}{1}$ *M*. P^4 with three outer cusps. M_1 lacking metaconid and talonid. M^1 rudimentary. Condylar and carotid foramina joined with foramen lacerum posterius. Mastoid process small, and pressed

against the ossified bulla. Symphysis wanting flanges. Recent in the Old World and America, fossil in the Upper Miocene. *F. media*, *F. pygmaea* Gerv., in the Sansan beds; *F. turnauensis* Toula in Styria; *F. zitteli* Gaillard at La Grive St. Alban. Lower Pliocene. *F. attica* Wagn. Pikermi. *F. antediluviana* Kaup. Eppelsheim. *F. brevirostris* Croiz. Pliocene of Roussillon and Maragha. *F. pardinensis*, *F. arvernensis* Croiz. Tuscany and Auvergne. *F. leo* (*L. spelaea* Goldf.), *F. pardus*, *F. lynx*, etc.; in the Pleistocene of Europe. *F. atrox* Leidy, Miocene of Nebraska. *F. onca* Linn. in South America, *F. chaus* in East Indies.

Suborder C. PINNIPEDIA. Seals and Walruses.[1]

Carnivora in which the limbs are adapted for an aquatic life, the proximal segments being short, the distal elongated and webbed between the digits. Dentition complete, P and M homodont, either conical, or consisting of a high cone with anterior and posterior accessory cusps; the two most posterior molars generally absent, as are carnassials; incisors conical commonly less than 3 3; canines strongly developed. Extremities pentadactyl, first and fifth digits of pes being larger than the others. Scaphoid fused with lunar and centrale. Cerebral hemispheres strongly convoluted.

The *Pinnipedia* show a great resemblance to terrestrial carnivores in anatomical and ontogenetic characters. Owing to their adaptation to an aquatic habitat, they have acquired to a certain extent a fish-like form of body, and their dentition has also become modified. A reduction in number and a greater simplification of the teeth is to be observed, associated frequently with the complication of the premolars The *Pinnipedia* inhabit the circumpolar regions of both hemispheres.

Fossil forms are rare, occurring first in the Miocene. Neither palaeontology nor ontogeny furnishes satisfactory clues concerning their origin. *Patriofelis* among creodonts is regarded by Wortman as a possible ancestor of the group, a marked resemblance lying in the structure of the astragalus. On account of the presence of the "Ursine" lozenge characteristic of the brain of the Arctoidea, Weber and others derive the *Pinnipedia* from the *Ursidae*.

The *Pinnipedia* may be divided into three families: *Otariidae*, *Phocidae*, *Trichechidae*. The *Otariidae* appear first in the Miocene of Oregon (*Pontoleon* True). *Otaria* occurs in the Tertiary and Pleistocene of Argentina, as well as in the Pleistocene of North America. *Arctocephalus* is found in the Pliocene of Victoria and Pleistocene of New Zealand. The *Trichechidae* are represented in the Upper Miocene of Maryland and of Europe, and in the Pleistocene of England, Belgium (also in the Pliocene), Holland and North America.

The *Phocidae* first appear in the Miocene of Egypt. In Maryland is found *Leptophoca* True. *Lobodon* occurs in New Jersey, *Phoca* in Virginia. In the Miocene of the Vienna Basin we have *Phoca vindobonensis* Toula. In Hungary, *P. holitschensis* Brühl; in South Russia, *P. pontica* Eichwald. In the Pliocene of Montpelier, *Pristiphoca* Gervais; in Belgium, *Monatherium* and *Prophoca*

[1] *Beneden, P. J. van*, Description des ossements fossiles des environs d'Anvers. Ann. Mus. Hist. Nat. Belgique, vol. i., 1877.—*Toula, F. Phoca vindobonensis.* Beitr. Palaont. Österr.-Ungarns, 1897.

Geological and Geographical Distribution of Carnivora.

	Lower Eocene.	Middle Eocene.	Upper Eocene.	Oligocene.	Lower Miocene.	Upper Miocene.	Pliocene.	Pleistocene.	Recent.
I. Creodontia									
1. *Oxyclaenidae*	N.A. E.	.....	.....	.....	.....	.....	.....	.....	.....
2. *Mesonychidae*	N.A. E.	N.A. E.	N.A.	} Af. ?	.....	.....	.....	.....	.....
3. *Oxyaenidae*	N.A. E.	N.A.	N.A. E.		.....	.....	.....	.....	.....
4. *Hyaenodontidae*	N.A.	N.A. E.	N.A. E.	N.A. E. Af.	As. Af.	.....	.....	.....	.....
5. *Arctocyonidae*	N.A. E.	.....	.....	.....	.....	.....	.....	.....	.....
6. *Miacidae*	N.A.	N.A.	N.A. E. ?	.....	.....	.....	.....	.....	.....
II. Fissipedia									
1. *Canidae*	.....	.....	N.A. E.	N.A. E.	N.A. E. As.	N.A. E.	N.A. E. As.	N.A. S.A. E. As. Af. Au.	N.A. S.A. E. As. Af. Au.
2. *Ursidae*	.....	.....	.....	.....	.....	E.	N.A. E. As.	N.A. S.A. E. As. Af.	N.A. S.A. E. As. Af.
3. *Procyonidae*	.....	.....	.....	.....	N.A.	N.A. E.	N.A. S.A. E.	N.A. S.A.	N.A. S.A. As.
4. *Mustelidae*	.....	.....	.....	N.A. E.	N.A. E.	N.A. E. As.	N.A. S.A. E. As. Af.	N.A. S.A. E. As. Af.	N.A. S.A. E. As. Af.
5. *Viverridae*	.....	.....	E. ?	E.	E.	E.	E. As.	As.	E. As. Af.
6. *Hyaenidae*	.....	.....	.....	.....	.....	.....	E. As.	E. As. Af.	As. Af.
7. *Felidae*	.....	.....	E. ?	N.A. E.	N.A. Af.	N.A. E. As.	N.A. S.A. E. As. Af.	N.A. S.A. E. As. Af.	N.A. S.A. E. As. Af.
III. Pinnipedia									
1. *Otariidae*	.....	.....	.....	.....	.....	N.A. S.A.	S.A. Au.	N.A. S.A. Au.	N.A. S.A. Au.
2. *Phocidae*	.....	.....	.....	.....	.....	E. N.A. Af.	E. N.A.	E. N.A.	N.A. S.A. E. As.
3. *Trichechidae*	.....	.....	.....	.....	.....	E. N.A.	E.	E. N.A.	N.A. E. As.

N.A. = North America, S.A. = South America, E. = Europe, As. = Asia, Af. = Africa, Au. = Australia.

Van Beneden; in the Pliocene of Orciano, Italy, *Monachus*; in Antwerp, *Phoca*, *Palaeophoca*, etc. *Phoca* (Fig. 108) is also present in the Pleistocene of Scotland, England, Norway and North Germany.

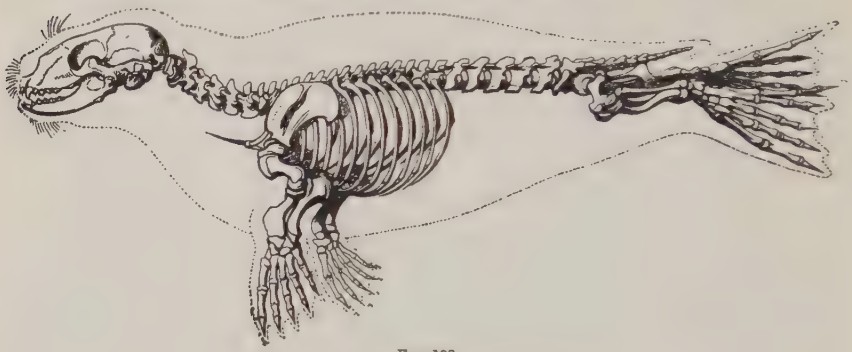


FIG. 108.
Phoca groenlandica Nilss. North Sea. (After Owen.)

Order IV. CETACEA. Whales.[1]

Naked, smooth-skinned, pisciform aquatic mammals with cylindrical body. Head not differentiated from trunk. Nostrils far back on the upper surface of the head. Fore-limbs fin-like, hind-limbs vestigial. Sacrum lacking. Caudal fluke horizontally expanded. Mammary glands in the inguinal region close to genital opening. Uterus bicornis, placenta diffuse, adeciduous.

The whales constitute an order widely distinct from other mammals owing to their mode of life and their fish-like form of body.

A thick, smooth skin envelops the entire body, and beneath this a layer of fat is developed, which is a poor conductor of heat. Hairs are either entirely lacking in the adult stage or are reduced in several genera to a few bristles on the face.

Cetacean bones, particularly the vertebrae, are distinguishable by their spongy, porous texture, and are usually impregnated with oil. The vertebral epiphyses remain distinct from the centra for a considerable period, as do also those of the limb bones. The anterior and posterior vertebral faces are smooth and united by a thick layer of cartilage. The cervical vertebrae are of the usual number, though frequently compressed, disk-like and occasionally more or less fused.

[1] *Abel, O.*, Hautbepanzerung fossiler Zahnwale. Beitr. Paläont. Öster.-Ung., 1901.—Les Dauphins longirostres du Boldérien. Mém. Musée Roy. Belgique, vol. i., 1900; vol. ii., 1902.—Les Odontocétés du Boldérien. *Ibid.* vol. iii., 1905.—Die fossilen Platanistiden des Wiener Beckens. Denkschr. Akad. Wiss. Wien, vol. lxviii., 1899.—*Beneden, P. J. van*, and *Gervais, P.*, Ostéographie des Cétacés vivants et fossiles. Paris, 1868–80.—*Van Beneden, P. J.*, Description des ossements fossiles d'Anvers. Ann. Musée d'Hist. Nat. de Belgique, vol. i., 1877–86.—*Brandt, J. F.*, Die fossilen und subfossilen Cetaceen Europas. Mém. Acad. St. Pétersb., vii. sér., vol. xx., 1873; vol. xxi., 1874.—*Capellini, Giov.* Mem. Accad. Sci. di Bologna, 2ª ser., vol. iii., 1864; 4ª ser. vol. iii., 1882; vol. iv., 1883; 5ª ser., vol. i., 1891; 6ª ser., vol. i. 1901.—Mem. Accad. dei Lincei, 1885, 4ª ser., vol. i.—*Cope, E. D.*, The Cetacea. Amer. Naturalist, 1890.—*Eastman, C. R.* Bull. Mus. Compar. Zool. Cambridge, Mass., vol. l., 1906; vol. li. 1907.—*Owen, R.*, Monograph of the British fossil Cetacea from the Red Crag. Palaeont. Soc. London, 1870.

Succeeding the cervicals are 9-16 dorsal, 3-24 lumbar and 18-30 caudal vertebrae. A sacrum is lacking. The upper arches and ossified epiphyses of the trunk vertebrae are separated for a long time from the centrum and are fused with the latter only in old age. The zygapophyses become more or less vestigial. The diapophyses, on the other hand, are long and well developed in the lumbar region. The ribs of *Cetacea* are distinguished from those of other mammals by their loose union with the vertebral column and sternum. The latter bone in baleen whales consists of a simple, broad, shield-like piece, often concave anteriorly. In the Odontocetes there are two to five bones, arranged in linear series.

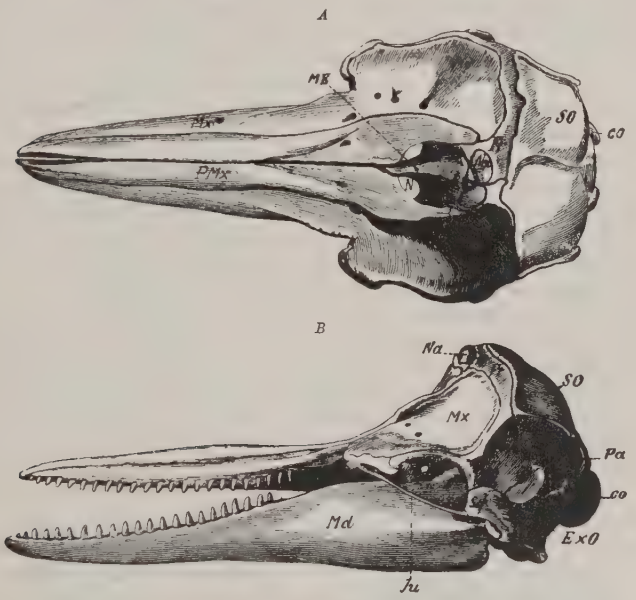


Fig. 109.

Tursiops (*Delphinus*) *tursio* Fabr. sp. Atlantic Ocean. *A*, Superior aspect of skull. *B*, Lateral aspect of the same. (After Cuvier) 1/6. *Pmx*, Premaxilla; *Mx*, maxilla; *ME*, mesethmoid; *Na*, nasals; *N*, nares; *Fr*, frontal; *Pa*, parietals; *Ju*, zygomatic or jugal arch; *Sq*, squamosal; *SO*, supraoccipital; *co*, condyle; *Exo*, exoccipital; *Md*, mandible.

The skull (Fig. 109) undergoes some very striking changes, due to the mode of life, and consists of light, large-celled, thin bones. The brain-cavity is remarkable on account of its extraordinary height, considerable breadth, but extreme shortness. Since it becomes contracted above, the brain has the shape of a foreshortened cone, with rounded contour. The very strongly convoluted hemispheres of the cerebrum almost completely cover the cerebellum. The olfactory lobes are either entirely lacking or only weakly developed; the nasal openings are destitute of turbinals and do not serve as olfactory organs but entirely for breathing. With the exception of *Zeuglodon* the parietals do not meet in a sagittal suture, and are in contact in the medial line only in the case of the baleen whales. But also among these the extremely large supraoccipital overlies the parietals and interparietal and

constitutes the main part of the cranial roof. Through the shortening and lateral compression of the parietals, the supraoccipital and interparietal of the Odontocetes and some of the baleen whales meet the very short frontal, which broadens laterally on both sides into large bony plates extending over the orbits. The high occiput, sloping posteriorly, is formed entirely by the supraoccipital. The deeply set squamosal (*sq.*) has a well-developed prominence, looking forwardly and upwardly, which joins with the posterior wing of the frontal and which serves as a support for the zygomatic arch, bounding the elongated orbits, and which, in the case of the Odontocete whales, is thin and rod-like (*ju.*), and in the baleen whales is strongly developed.

The very elongated, usually flattened and narrowed muzzle is composed of the frequently asymmetrical premaxillaries, the maxillaries, vomer and mesethmoid. The premaxillaries are either closely approximated in front or else leave vacuities above, which broaden out posteriorly. At the hinder end of these bones and adjacent to the frontals are the almost perpendicular, or steeply inclined nostrils which function as blow-holes. The external nostrils are overhung by short, well-developed nasals in the case of the baleen whales; but among Zeuglodonts the nasals are elongated; Odontocete whales have the nasals so reduced that frequently only a bony protuberance remains. The embryos still retain the primitive structure. The backward displacement of the nostrils has caused the extension of the maxillary and premaxillary bones behind the orbits and the shortening of the frontals, parietals and nasals, which are also crowded to the side of the skull. The brain-case is bounded anteriorly by the almost perpendicular, broad mesethmoid (*me.*). All recent *Cetacea* have the maxillary enclosing the premaxillary on the sides throughout its length except on the extreme tip of the snout; the fossil *Zeuglodontidae* and *Squalodontidae* have the premaxillary projecting over the maxillary in front and set with teeth on its lower surface. Only a few baleen whales and *Physeteridae* have a lachrymal bone.

The inferior portion of the snout is formed principally by the horizontal branches of the maxillary, though the vomer, a narrow bone lying in the median line between the two portions of the maxillary, frequently takes part in forming the roof of the mouth. The short, strip-like palatal bones bound the maxillary bone behind and are in contact posteriorly with the well-developed pterygoids, which meet in the median line, and increase the length of the bony palate besides forming the walls of the choanae. Of especial interest are the auditory bones (periotic and tympanic) (Fig. 110) placed between the squamosal and the exoccipital. They are extraordinarily massive, are only loosely united with the other bones of the skull, and therefore are easily lost in the fossil state. Isolated periotic and tympanic bones (cetoliths) are found in almost all strata yielding Cetacean remains, and ear-bones of whales have also been dredged from the floor of the ocean.

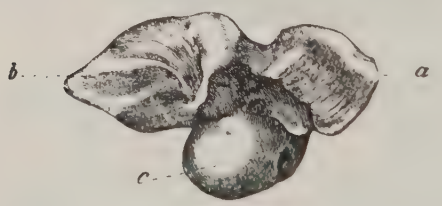


FIG. 110.

Left periotic of *Globicephalus uncidens* from the Crag of Orford, as seen from the side directed toward the tympanic. *a*, Posterior, and *b*, anterior process; *c*, hemispherical portion.

The dentition of *Cetacea* consists, for the most part, of conical, similar, single-rooted teeth, which frequently develop in very great number (as many as sixty in each jaw). Only in the case of the Zeuglodonts and Squalodonts are the two- or three-rooted hind teeth distinguished from the one-rooted front teeth by a laterally compressed crown. The baleen whales have no teeth at all. The male of the Narwhal has a strong tusk, directed toward the front, in the right upper jaw. Dental succession does not occur, even though, in the case of several toothed whales, the second dentition is present in a rudimentary state; this second set of teeth, however, never breaks through the skin. From the original heterodont dentition a homodont condition develops. Homodonty and reduction of teeth begin at the front end of the rostrum. At first the teeth of the upper jaw disappear, then those of the lower jaw become lost, until the former presence of teeth is only indicated by a dental groove.

Owing to their aquatic mode of life the *Cetacea* have undergone a most extraordinary transformation of limb structure, the appendages having become modified into flippers resembling the fins of extinct marine reptiles. The clavicle is lacking, as is also a separate coracoid. The scapula is distinguished by its unusually broad, flat and comparatively short form. The humerus is short and massive, provided on the proximal end with a hemispherical head. The distal end is furnished with two facets, forming an obtuse angle, on which the laterally compressed forearm bones fit. These are movable neither on the humerus (except in the case of *Zeuglodon*) nor on each other. The *Cetacea* have five digits, with the exception of a few baleen whales, which are remarkable for having lost the third instead of the first digit through specialisation. The phalanges are not articulated, but are united by cartilage and fibrous tissue, and the digits are entirely surrounded by a common layer of skin. They consist of elongated, flattened phalanges, truncated at the extremities, and slightly constricted in the middle. The number of these phalanges in the second and third digits is as many as from nine to fifteen. The hind-limbs and pelvis are either totally degenerate or consist only of small vestiges of the ischium and femur not showing externally.

A large, horizontal caudal fin, supported not by bony structure but by a compact intertwining of fibres, serves as the chief locomotive organ instead of limbs. Polygonal, calcified plates on the dorsal and ventral fins of certain whales have led to the theory, supported by Kükenthal and Abel, that these represent the remnants of a bony armour, which could, however, not have served as a complete body covering.

In spite of all striking similarities between *Cetacea* and fishes and the marine reptiles, due to environmental influences, the skeleton of this order is fundamentally mammalian and shows no resemblances whatsoever to that of fishes or reptiles. The *Cetacea* evolved, not from aquatic reptiles, but in all probability from carnivorous, placental land mammals with normal heterodont dentition $\frac{3.1.4.3.}{3.1.4.3.}$. They frequently attain a gigantic size and are either pelagic or live near the shores.

Fossil *Cetacea* appear first in the Eocene with the extinct form, *Zeuglodon*, become more widely distributed in the Miocene and Pliocene, and at this period become much diversified.

Suborder A. ARCHEOCETI Flower.

External nostrils opening forwardly and upwardly and situated on the upper side of the snout. Nasals short. Maxilla not extending over the frontals. Teeth in premaxillary, maxillary and mandible; the anterior teeth with one root, the posterior with two, and in the upper jaw frequently with three roots.

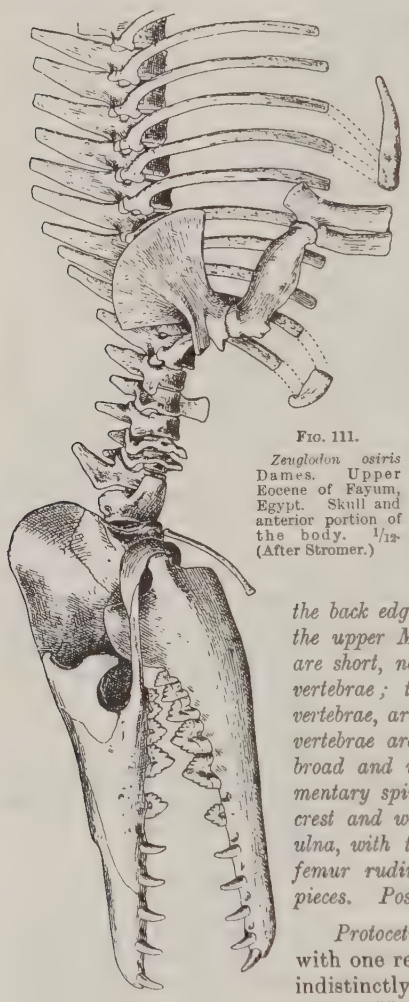


FIG. 111.

Zeuglodon osiris Dames. Upper Eocene of Fayum, Egypt. Skull and anterior portion of the body. 1/12. (After Stromer.)

Family 1. Zeuglodontidae.[1]

Head elongate, brain-case small, temporal fossa widely extended, sagittal crest well developed. Parietals elongate, narrow and forming part of cranial roof; frontals broad and short, roofing over the orbits. Zygomatic arch rod-like. Snout long and compressed. Nasals long and narrow. Mandible long, low and without well-defined symphysis. Teeth differentiated: $\frac{3.1.4.3\text{-}2.}{3.1.4.3.}$, *and complete milk dentition present. Front teeth* I_1-P_2 *(incl.) separated; the back teeth very compactly set. I, C and frequently* P_1 *all conical with one root; hind teeth with two roots.* P_2 *to* P_4 *have cusps on the front and rear edges and M has a few on the back edge. The two hind upper P, at times also the upper M, are three-rooted. The cervical vertebrae are short, not fused together. Usually twelve dorsal vertebrae; the last of these, as well as the lumbar vertebrae, are frequently very much elongated. Caudal vertebrae are short. Ribs with two heads. Scapula broad and with acromion, coracoid process and rudimentary spine. Humerus short, with massive deltoid crest and well-developed trochlea. Radius in front of ulna, with two distal articular surfaces. Pelvis and femur rudimentary. Sternum composed of several pieces. Possibly dermal armour was present.*

Protocetus Fraas. $\frac{3}{3}$ *M.* The two last *P* only with one rear cusp, *M* also with front cusps. *C*-P_2 indistinctly two-rooted, P^3 to M^3 each with three roots. Vertebrae small, like those of carnivores. Middle Eocene; Mokattam, Egypt. *P. atavus* Fraas.

[1] *Andrews, C. W., Pappocetus.* Proc. Zool. Soc., 1919.—*Fraas, E.*, Neue Zeuglodonten aus dem Mitteleozaen von Mokattam. Geol.-Paläont. Abhandl., vol. x., 1904.—*Lucas, F. A.*, Notes on the Osteology of Zeuglodon. Amer. Naturalist, 1895.—*Müller, Joh.*, Über die fossilen Reste der Zeuglodonten von Nord-Amerika, Berlin, 1894.—*Stromer, E. v.*, Zeuglodontenreste aus dem Mitteleocaen des Fayum. Beitr. Paläont. Österr.-Ung., vol. xv., 1903.—Die Archäoceti des ägyptischen Eocaens. *Ibid.* vol. xxi., 1908.

Eocetus (*Mesocetus*) Fraas. With large, elongated lumbar vertebrae. *E. schweinfurthi* Fraas. Same horizon and locality.

Pappocetus Andrews. Dentition complete; cheek teeth with strong basal cingulum. Eocene; S. Nigeria.

Zeuglodon Owen (Fig. 111) (*Basilosaurus* Harlan, *Dorudon* Gibbes, *Pontobasileus* Leidy). $\frac{2}{3}$ *M.* P_2-P_4 with several cusps on anterior and posterior borders, *M* having them only on posterior border. Upper Eocene of Egypt. *Z. osiris* Dames, and *Z. zitteli* Stromer, with short lumbar vertebrae, and *Z. isis* Beadnell (*Prozeuglodon atrox* Andrews) with elongate lumbar vertebrae. Eocene of Alabama. *Z. cetoides* Owen; *Z. serratus* Gibbes; *Z. brachyspondylus* Müller. Eocene of England. *Z. wanklyni* Seeley. *Z. harwoodi* Sanger, from the Eocene of South Australia, and the so-called species of *Zeuglodon* described by Wiman, from Seymour Island, and also *Kekenodon omata* Hector, from the Miocene of New Zealand, are probably *Squalodontidae.*

Suborder B. ODONTOCETI. Toothed Whales.

External nares confluent, forming a simple spoutlike blow-hole and situated far back on the head and directed upwards. Nasals reduced. Upper jaw broad posteriorly, and partly overlapping the frontals. Usually numerous teeth, which at times are reduced to a single pair. Front ribs with two heads. Sternum composed of two or more pieces of bone.

Family 1. Squalodontidae.[1]

Premaxillary, maxillary and mandible dentigerous. The front teeth are conical, with one root; the molars two- and three-rooted, compressed and having cusps on front and hind edges. Parietals form part of the roof of the brain-case.

Microzeuglodon Stromer. Supposed Eocene of the Caucasus. Only teeth and humerus known. *M. caucasicus* Lydekker sp.

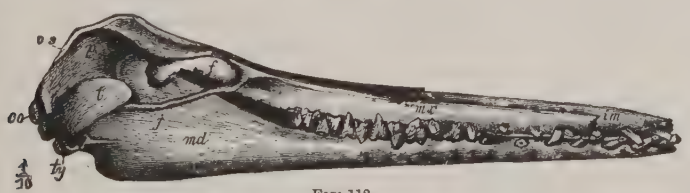


FIG: 112.

Squalodon bariensis Jourdan sp. Miocene. $^1/_{10}$. Restored skull from Bari in the Department of Drôme. (After Döderlein.) *co*, Condyle; *os*, supraoccipital; *f*, frontal; *j*, jugal; *t*, squamosal; *ty*, tympanic; *im*, premaxilla; *mx*, maxilla; *md*, mandible.

Neosqualodon Dal Piaz. With many multi-cuspid molars. Middle Eocene of Sicily. *N. assenzae* F. Major sp. *Squalodon* Grateloup (*Pachyodon*, *Arionius* Meyer; *Phocodon* Agassiz; *Rhizoprion* Jourdan; *Delphinodon* Leidy) (Fig. 112). $\frac{3.1.9\text{-}8.3.}{3.1.8.3 \div 2.}$. The last 7-8 teeth with two roots. In the Miocene, Pliocene of Europe and North America are found many different species; in the Oligocene of Bunde, Westphalia (*Phoca ambigua* Münster).

[1] *Beneden, P. J. van.* Mém. Acad. Roy. Belgique, 1853, vol. xxxv.; 1867, vol. xxxvii.—*Grateloup.* Actes Soc. Linn. Bordeaux, 1840, vol. ii.—*Jourdan. Rhizoprion Bariense.* Ann. Sci. Nat., 1867, 4e sér., vol. xvi.—*Lortet, L.* Archives Mus. d'Hist. Nat. Lyon, 1887, vol. iv.—*Paquier, V.* Mém. Soc. Géol. France. Paléont., vol. iv., 1894.—*Dal Piaz, G.*, Neosqualodon. Mém. Soc. Paléont. Suisse, vol. xxxi., 1904.—*Zittel, K. A.* Palaeontographica, 1877, vol. xxiv.

Prosqualodon Lydekker. Five teeth are two-rooted. *P. australis* Lyd. in Miocene of Argentina. *P. davidi* Flynn in Miocene of Tasmania.

Family 2. **Physeteridae** Flower.

Skull very asymmetrical. Premaxillary and maxillary in the later forms are toothless, lower jaw with a varying number of one-rooted, conical teeth. Frontals rising abruptly behind the nasals and forming a transverse ridge. Orbits are small. Lachrymal bones large. Lower jaw symphysis long among early forms, short among later. Anterior ribs with two heads. Recent and fossil in the Miocene, Pliocene and Pleistocene of Europe, North America and Australia.

Subfamily 1. Physeterinae.

Cervical vertebrae, with the exception of the atlas, fused into one. Teeth all of uniform size, originally with enamel.

Scaldicetus du Bus (*Balaenodon, Eucetus, Homoeocetus, Eudelphis, Palaeodelphis* du Bus; *Hoplocetus, Physodon* Gerv.). Miocene and Pliocene of Europe, North America and Patagonia. Three upper *I.* Nineteen teeth in the upper jaw and twenty-four in the lower.

Thalassocetus, Prophyseter Abel. Belgium. *Placoziphius* Beneden. Belgium and Italy. *Physeterula* Beneden. Miocene of Europe.

Physeter Linn., *Kogia* Gray. Recent, without upper teeth.

Subfamily 2. Ziphiinae.

One or two pairs of lower teeth enlarged. Atlas and axis one; the remaining cervical vertebrae are separate.

Palaeoziphius Abel (*Champsodelphis* du Bus; *Acrodelphis* Abel, *partim*). Lower jaw with 14 alveoli, 1 and 7 teeth enlarged. *Mioziphius* Abel (*Placoziphius* Gerv.). The two front teeth enlarged. These two genera occur in the Miocene of Belgium.

Choneziphius Duvernoy; *Mesoplodon* Gervais (*Dioplodon* Gerv.; *Belemnoziphius* Huxley). Miocene and Pliocene of Europe and South Carolina and Recent. *Ziphius* Cuv.; *Berardius* Duvernoy; and *Hyperoodon* Lacép. Recent.

Family 3. **Eurhinodelphidae** Abel.

Rostrum very long, narrow and with very long toothless premaxillary. Skull slightly convex or with transverse ridge. Upper and lower jaws with many one-rooted teeth. Upper jaw thickened beneath the orbit and frontal often covered by the supraoccipital. All the cervical vertebrae are distinct. Anterior ribs have two heads.

Eurhinodelphis du Bus (*Priscodelphinus* du Bus). The most abundant of all whales in the Miocene of Belgium. Also in North America.

Family 4. **Acrodelphidae** Abel.

Rostrum originally long, but later foreshortened. Upper jaw often reaching to the front end of the rostrum. Teeth are polyodont, heterodont and one-rooted.

Temporal fossae uncovered, cranium slightly rounded, supraoccipital rather square. Cervical vertebrae distinct. Dorsal, lumbar and caudal vertebrae are long. Front ribs two-headed.

Subfamily 1. ARGYROCETINAE.

Skull rather flat. Frontals expanded over the top of the cranium. Rostrum very long. Teeth unusually numerous; those in front pointed, those in the rear conical.

Cyrtodelphis Abel (*Champsodelphis* Gerv.). Abundant in the European Miocene. *C. sulcatus* Gerv. sp.

Argyrocetus, *Pontivaga* and *Ischyrorhynchus* Ameghino and *Saurodelphis* Burmeister. In the Miocene and Pliocene of Argentina.

Subfamily 2. ACRODELPHINAE.

Skull flat, frontals narrow, rostrum long and teeth with small serrations.

Acrodelphis Abel (*Champsodelphis* Brandt, Gerv., *p.p.*; *Phocaenopsis* du Bus; *Delphinodon* Cope). Very abundant in the Miocene of Europe.

An almost complete skeleton of *Heterodelphis leionodontus* Papp was found in the Miocene (Leita Limestone) of the Sopron County of Hungary.

Priscodelphinus Leidy. *Rhabdosteus*, *Lophocetus*, *Zarhachis*, *Ixacanthus* Cope. Miocene of North America.

The subfamilies of *Iniinae* and *Beluginae* are not known as fossils. The former contains the long-snouted genera *Platanista*, *Inia*, *Pontistes* and *Pontoporia*, which only attain the length of 1 to 2 m., and inhabit the mouths of large rivers. The latter consists of the short-snouted genera *Beluga* and *Monodon*.

Family 5. **Delphinidae** Flower.

Short snout, premaxillary without teeth and surrounded by the maxilla. Upper and lower jaw have a varying number of conical, one-rooted teeth. The symphysis of the lower jaw is short. Orbits moderate. The anterior cervical vertebrae are fused. Front ribs have two heads.

The dolphins, in the modern fauna, comprise the largest number of forms of the *Odontoceti*. The many genera of this family are found in all seas and frequently inhabit also the mouths of large rivers. Fossil remains occur sparingly in the Miocene, Pliocene and Pleistocene of Europe and America and are referable to the modern *Delphinus* Linn., *Steno* Gray, *Tursiops* Gervais (Fig. 109), *Orca* Gray, *Pseudorca* Reinh. and *Globicephalus* Lesson (Fig. 110), as well as to certain extinct genera. *Protophocaena* Abel occurs in the Miocene of Belgium, *Palaeophocaena* Abel is known from the Crimea, and *Delphinopsis freyeri* Joh. Müller with dermal ossicles is found in Croatia. All of these belong to the *Phocaenini*. *Pithanodelphis* Abel, a dolphin, has been described from the Miocene of Belgium.

Suborder C. MYSTACOCETI. Whalebone Whales.

Skull symmetrical. Nasals short and overhanging to a certain extent the two blowholes. Functional teeth lacking. Upper jaw provided with whalebone and very broad posteriorly, but not projecting over the frontals. Lachrymal bones small. Mandibular extremities not meeting in a symphysis, but separated and slightly convex. Almost all

the ribs with but a single head. Sternum is short, broad, and consisting of one piece and joined only to the foremost ribs.

The baleen whales are the most remarkable and highly specialised group of *Cetacea* on account of the degeneration of the jaws and the development of baleen in place of teeth. The only indication that this form is derived from toothed ancestors is the occurrence of small, weak teeth hidden in the gums of the embryo. In skull formation, especially in the development of nasals, frontals and parietals, the Mystacocetes are more primitive than the Odontocetes.

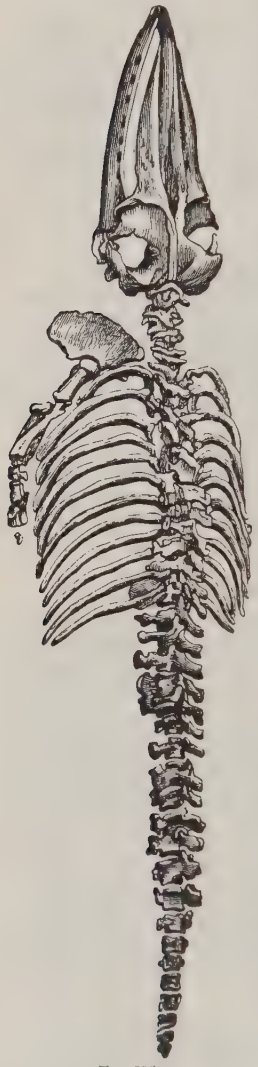


Fig. 113.

Plesiocetus cuvieri Desm. Pliocene of Monte Pugnasco near Piacenza. 1/40. (After Cuvier.)

Family 1. **Balaenopteridae.** Fin Whales.

Head less than one-fourth of the total length of the whole body. On the lower side of the body there are many furrows. Dorsal fin present. Manus with four digits, narrow and rather long. Baleen short and broad. Cervical vertebrae articulating, not fused, their centra rather long. Tympanic long and much inflated and rounded on all sides. Recent and fossil in the Miocene and Pliocene.

Plesiocetus v. Bened. (Fig. 113). In the Miocene of France and southern Germany. Complete skeletons 6 m. in length have been found in the Pliocene of northern Italy.

Cetotherium Brandt (*Aulocetus* v. Bened.). Miocene. *Heterocetus, Herpetocetus, Mesocetus* van Bened. *Balaenoptera* Lacép. *Megaptera* Gray, in the Pliocene of Belgium and England. A complete skeleton of *Mesocetus* has been found in Hungary, Sopron County.

From the Miocene of North America *Siphonocetus, Cetotherium* and *Mesoteras* Cope are known.

Family 2. **Balaenidae.** Right Whales.

Skull very large, comprising, at least, one-fourth of the entire length of the body. Skin on the ventral surface smooth. No dorsal fin. Manus with five digits, broad and foreshortened. Baleen very long and narrow. Lower jaw narrow, very convex, flattened on the inner side and having spherical condyles. All, or almost all, of the cervical vertebrae are fused. Lumbar and caudal vertebrae short. Tympanic almost square and angular and but slightly inflated.

The Right Whales are restricted at the present day to the Polar regions of both hemispheres. Fossil forms of the genus

Balaena Linn. are found sparingly in the latest Tertiary deposits and in the Pleistocene of Europe.

Order V. EDENTATA (Bruta Linn.[1])

Dentition usually consisting only of prismatic cheek teeth without enamel, sometimes entirely wanting. The terminal phalanges are long, pointed and laterally compressed claws, seldom hoof-like. Skin covered with hair, horny or bony plates.

The *Edentata* constitute among placental mammals a distinct group and were ranked by Cuvier as parallel to the Ungulates and Unguiculates. The *Edentata* differ principally from other mammals in that they have (1) a dentition, as a rule, monophyodont, consisting of prismatic teeth and lacking incisors and canines; (2) no enamel is present in the teeth of all recent forms; (3) a variable number of dorsal and caudal vertebrae is observed in several genera; (4) fusion of the ischium and sacral vertebrae occurs; (5) there is a common urinary and genital duct in the female; and (6) a very well developed osseous exoskeleton is present in armadillos and their allies.

As to the origin of the group, *Nomarthra* are known to have existed in the Eocene or Oligocene of Europe, and armadillos were abundant during the same periods in South America. The *Taeniodonta* of the North American Lower Eocene have been claimed as ancestors of the *Gravigrada*. Although the time of their appearance would favour this supposition, there are serious morphological objections, and this view is not generally accepted. The first true *Gravigrada* are found in the Pyrotherium beds (Lower Miocene) of South America.

The vertebral column consists of well-differentiated cervical, dorsal, lumbar, sacral and caudal regions. As a rule, the cervical vertebrae are 7 in number, rarely 9. The number of dorsal vertebrae varies from 12 to 24, that of the lumbar from 3 to 9. In the *Glyptodontia* several of the dorsal vertebrae, together with their spinous processes, are fused to form an immovable tube. This is also the case with the lumbar and post-sacral vertebrae. The posterior caudal vertebrae also become a more or less inflexible mass of bone on account of the anchylosis of the centra; and the anterior and posterior cervical vertebrae are likewise fused together.

The skull is often elongated, and at other times very short and deep. In most cases the top of the skull is rounded or flat, and only in the *Gravigrada* do the parietals sometimes form a small crest. The premaxillary bones are very weakly developed in all *Edentata*, and rarely serve as a lateral boundary of the large nostrils. The zygomatic arch is

[1] *Ameghino, Flor.*, Contribución al conocimiento de los mamíferos fósiles de la Republica Argentina. Actas Acad. Nac. Ciencias Cordoba, 1889.—Les Édentés fossiles de France et d'Allemagne. Anal. Mus. Nac. Buenos Aires, vol. xiii., 1905.—*Burmeister, H.* Anal. Mus. Nac. Buenos Aires, Entrega i-xii.—*Cope, E. D.*, The Edentata of North America. Amer. Naturalist, 1889.—*Filhol, H.* Annales Scienc. Nat., Zoologie et Paléont., vol. xvi., 1894.—*Lydekker, R.*, Paleontologia Argentina, iii. Anal. Mus. La Plata, 1894.—*Owen, Richard*, Description of the skeleton of an extinct gigantic sloth (*Mylodon robustus*), 1842.—On the Megatherium. Philos. Trans., 1851–59.—On Glyptodon. Proc. Geol. Soc., iii., 1839.—*Reinhardt, J.* Vetensk. Selsk. Skin. Kjøbenhavn., 5. Raekke xi.; xii.—*Scott, W. B.*, Reports of the Princeton Univers. Exped. to Patagonia. Palaeontology, vol. v., 1903, 1904.—*Brown, Barnum*, Brachyostracon, a new genus of Glyptodonts from Mexico. Bull. Amer. Mus. Nat. Hist., 1912, vol. xxxi.

either complete or interrupted, sometimes even rudimentary. It is distinguished, in the *Gravigrada*, *Tardigrada* and *Glyptodontia*, by a long process directed downward, and another less strongly developed one which is directed upward and backward.

Almost all edentates are monophyodont. Since milk-teeth precede the permanent dentition in the genera *Tatusia* and *Orycteropus*, it may be concluded that the ancestors of the *Edentata* were diphyodonts. The molars of the upper and lower jaws are similar or but slightly differentiated. They number from 4 to 10, sometimes even more. They are composed of dentine and an outer layer of cement. The dentine of the tooth consists, as a rule, of layers of varying hardness and different composition. The outer and hardest layer, traversed only by very fine dentine canals, surrounds a central vasodentine core, perforated by many coarse canals. The cheek teeth of *Edentata* are prismatic in form and attain frequently to a considerable height. They are without roots and open below, growing continually as their crowns are worn down. These last are most often worn down evenly, seldom obliquely; or transverse or oblique ridges may be formed. Not infrequently a part or all of the teeth possess on the outer or inner side, or on both, vertical furrows, which constrict the tooth and in the Glyptodonts convert it into a series of pillars connected by two or three narrow bridges.

The fore- and hind-limbs are sometimes equally well developed, but in general the hind-limbs are much more robust than the fore, and in the Glyptodonts much longer as well. The high median crest of the scapula terminates in a very long, overhanging acromion, which, in the *Gravigrada*, even fuses with the unusually well developed coracoid process. Adjoining this crest and slightly distant from the posterior surface of the scapula is a second, rather weak crest. Only the *Gravigrada* and a few armadillos possess a clavicle.

The humerus almost always has an entepicondylar foramen and a very well developed deltoid crest. Radius and ulna remain separate. The carpus has a centrale only in *Manis*, and consists usually of seven separate carpal bones and one pisiforme. Not infrequently there is a fusion of the magnum and trapezoid, or of the scaphoid and lunar, or in other cases the trapezium fuses with the scaphoid or the first metacarpal. In some cases all of the metacarpals are developed, or again, only four, and very seldom but three are functional. The digits are of varying lengths, five to three bearing phalanges, of which the terminal ones are developed as narrow, long, compressed and usually sharp claws.

The pelvis of the sloth and *Gravigrada* is wide anteriorly, but narrow and elongated in all other edentates. Except in *Orycteropus*, the unusually well developed ischia are joined with the caudal prolongation of the sacrum. The pubic bones are long and slender, the symphysis short, the obturator foramen large. The tibia and fibula are in some cases separate, in others they become fused distally or at both ends.

The tarsus and hind-limb of *Orycteropus*, ant-eaters and armadillos are usually pentadactyl; in the remaining forms the outer and inner metatarsals are frequently degenerate. The calcaneum has an elongated, rough tuber, the astragalus a concave trochlea for the articulation of the tibia, and on the outer surface a groove for the conical process of the fibula. The first and second phalanges are short, at times fused or united with one of the meta-

tarsals. The terminal phalanges are sometimes claw-like, sometimes broad and hoof-like, as in *Glyptodontia*.

The brain-case of the edentates is of moderate size; the brain of the several families differs considerably, however, in that the cerebrum may be either smooth or furrowed and the corpus callosum small or large.

In Old World forms the genital organs recall those of the *Ungulata*. The testicles are situated in the groin. The penis is external, the uterus is bicornuate, the vagina is undivided and the placenta is diffuse or broad and zone-like. American edentates have the testicles in the abdominal cavity between the rectum and bladder, the penis is small, the uterus is globular, and the placenta dome-shaped. The Old World forms are grouped as *Nomarthra*, and American edentates are designated as *Xenarthra*.

Suborder A. NOMARTHRA Gill.

The Old World edentates are distinguished by the simple articulation of the dorsal and cervical vertebrae. The family *Orycteropodidae* is represented in the Lower Pliocene of Bessarabia, Samos and Pikermi by a fossil form, *Orycteropus gaudryi* Forsyth Major, and also by a humerus (*Palaeorycteropus quercyi* Filhol) in the Phosphorites of Quercy. This horizon yields also the skull of *Leptomanis edwardsi*, and the humerus, femur and tibia of *Necromanis quercyi* Filhol. A form somewhat resembling *Orycteropus*, and also *Manis*, known as "*Lutra*" *franconica* Quenstedt, from the Miocene fissure deposits of Solenhofen, is called *Teutomanis* and *Galliaetatus* by Ameghino.

A metacarpal of very similar conformation is also known from the Miocene of Mont Ceindre, near Lyons. The indications are, as far as these incomplete remains show, that the apparently widely separated families of *Orycteropodidae* and *Manidae*, on the one hand, and the *Dasypodidae*, on the other, have a common ancestor.

Suborder B. XENARTHRA Gill.

The *Xenarthra*, distinguished by the accessory articulation of the posterior dorsal and cervical vertebrae, comprise two "tribes" or subdivisions: (1) the *Anicanodonta*, without or, at the most, with only vestigial dermal armour, and (2) the *Hicanodonta*, with a covering of bony or horny plates.

Tribe 1. ANICANODONTA Ameghino.

Of the families which constitute this tribe the *Myrmecophagidae* and *Bradypodidae* are represented only by very incomplete remains in the Pleistocene of South America. The extinct family *Gravigrada* is abundantly represented by fossil remains in the Tertiary of Patagonia and in the Pleistocene of South America. In North America this family is confined to the Pliocene and Pleistocene. It may have originated from the *Taeniodontae* of the Early Eocene of North America.

Family 1. **Taeniodontae** Cope. (*Ganodonta* Wortman.)

The number of I always reduced, C large, P and M usually with roots, and more or less completely covered with enamel. Vertebral articulation rather simple. Lower Eocene of North America. Puerco to the Wind River beds.

The skull and the massive extremities are very similar to those of the *Gravigrada*. The primitive dentition, also, may very readily have given rise to that of the *Gravigrada*. The slight difficulty in tracing this line of descent, which lies in the fact that the *Gravigrada* occur already in the early Tertiary of Patagonia, is surmounted if we assume that only the species of the Torrejon beds are ancestral to the South American forms, and that those of the Wasatch and Bridger formations became extinct without leaving any descendants. The *Taeniodontae* possibly have a common origin with the *Tillodontidae*, a family here placed among the Insectivores.

The humerus is stout and provided with a well-developed deltoid crest and entepicondylar foramen. The thick ulna has a high olecranon. The form and mode of articulation of the carpals, metacarpals and phalanges closely agree with those of the *Gravigrada*, especially *Mylodon*, as does also the flattened ilium. Only the astragalus differs markedly on account of its primitive form—*i.e.*, having a long neck—from that of the *Gravigrada*. The gradual increase in accessory vertebral articulation, however, helps to establish their close relationship.

Subfamily 1. Conoryctinae.

$\frac{2?1.4\text{-}3.3.}{2.1.4.3.}$ *Skull long, low and with sagittal crest. Lower jaw elongated, and the articulation not much higher than the top of the teeth. I small, C long, P_3 and P_4 not placed transversely. Upper M tritubercular, lower with four or five cusps, and talonid somewhat lower than the trigonid. All the teeth are brachyodont and rooted. The crown of the teeth is rapidly worn down.*

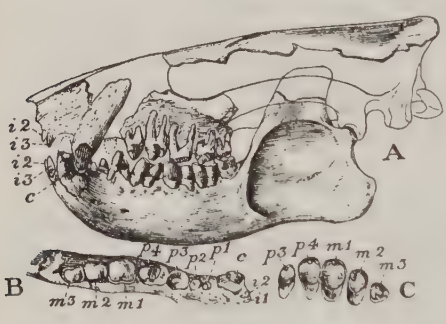


Fig. 114.

Conoryctes comma Cope. Lower Eocene of Torrejon beds, New Mexico. *A*, Skull and lower jaw. *B*, Lower dentition. *C*, Upper molars. 1/3. (After Wortman.)

Onychodectes Cope. $\frac{4}{4}$ *P*, lower *M* with paraconid. Lower Eocene; Puerco formation of New Mexico.

Conoryctes Cope (Fig. 114). $\frac{3}{4}$ *P*. M^3 very small, lower *M* with paraconid. Lower Eocene; Torrejon beds.

Subfamily 2. Stylinodontinae.

$\frac{1.?1.4.3.}{1.?1.4.3.}$ *Skull and lower jaw short. Articulation of the lower jaw much higher than the top of the teeth. C large, with very long root or with persistent pulp. P_3 and P_4 placed transversely. Vertebrae with secondary zygapophyses.*

Hemiganus Cope. $\frac{2.1.4.3.}{\quad}$. Upper *C* entirely covered with enamel, but lower *C* only covered on the anterior surface. *P* and *M* with roots. Basal Eocene; Puerco.

Psittacotherium Cope (Fig. 115). Upper and lower *C* have enamel only on the front surface and are rooted. Roots of *P* and *M* fused. $\frac{3}{3}$ *P*. Lower

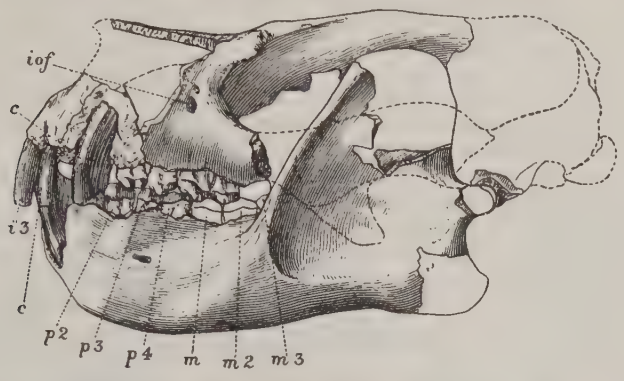


Fig. 115.

Psittacotherium multifragum Cope. Lower Eocene of Torrejon beds, New Mexico. Skull and lower jaw. 1/3. (After Wortman.)

Eocene; Torrejon. The skull of *P. multifragum* Cope is quite well known. It resembles that of *Megalonyx*.

Calamodon Cope (*Dryptodon* Marsh). $\frac{\text{———}}{1.1.4.3.}$ *C* with persistent pulp and resembling a rodent's canine. *P* and *M* with roots. *M* with four cusps forming two ridges. Lower Eocene (Wasatch); Wyoming. Possibly also in the Fort Union beds of Montana. Represented in the Middle Eocene Bohnerz of Egerkingen by a single tooth, named *C. europaeus* by Rütimeyer.

Stylinodon Marsh. All *P* and *M* are hypsodont without roots, and having enamel only in bands. Middle Eocene (Bridger beds); Wyoming. *S. mirus* Marsh.

Family 2. **Gravigrada**. Giant Sloths.

Extinct, large and plump herbivorous forms with long cylindrical skull. Zygomatic arch very strong, with downwardly directed process. $\frac{0.5\text{-}4.}{0.4\text{-}3.}$ *Teeth cylindrical. Tail unusually thick and long. Limbs stout and moderately long. Manus adapted for grasping, and pes plantigrade. Astragalus flat, sometimes with a short neck and distally truncated.*

The *Gravigrada* comprise the plumpest and clumsiest of all *Edentata*, and are distinguished from modern sloths by their long skull, the stronger zygomatic arches, and the long unusually powerful tail serving as a prop, the short, stout extremities, and frequently also by their considerable size. They are found in the Tertiary and Pleistocene of South America and in the Pliocene and Pleistocene of North America.

The oldest form is the very imperfectly preserved *Protobradys* Ameghino from the Notostylops beds of Patagonia. From the Miocene of Santa Cruz, on the other hand, are known remains of all three subfamilies *Megatheriinae*,

Megalonychinae and *Mylodontinae*, and among these the *Megalonychinae* are much diversified. These older forms are almost without exception much inferior in size to their Pleistocene relatives. Dermal ossification is not observable in any one of these forms. The dental formula is always $\frac{5}{4}$, and the first tooth in both jaws is always canine-like. The skull is distinguished by a long snout and a large brain-case. The trunk and scapula are more like those of *Bradypodidae* (*Choloepus*) than of the Pleistocene *Gravigrada*. The limb bones are always more slender, and the humerus is invariably provided with an entepicondylar foramen. Fusion of the carpals, tarsals or phalanges never occurs. The middle metapodial is, however, much shorter and thicker than the others, but the two outer ones are much less specialised than in the later Gravigrade forms, because the outside of the foot does not rest on the ground. The Miocene *Gravigrada* approach the *Bradypodidae* and *Myrmecophagidae* in exhibiting many similar skeletal structures.

Subfamily 1. Megatheriinae.

$\frac{5}{4}$ cheek teeth prismatic, quadrangular and closely set, the last one somewhat smaller than the rest. The posterior branch of the alveolar canal opens on the inner side of the lower jaw.

Megatherium Cuv. (Fig. 116). The first complete skeleton was exhumed in 1789 in Argentina, and sent to Madrid. Besides *M. americanum* Blumb. (= *M. giganteum* Pander), other species in the Pleistocene of Argentina, Brazil, Chile, Ecuador, Central America and the southern United States are known.

Fig. 116.

Megatherium americanum Blumb. Pampas formation (Pleistocene), Argentina. Superior aspect of lower jaw. 1/8. (After Owen.)

Nothrotherium Lydekker (*Coelodon* Lund). A considerably smaller form than *Megatherium*. Pleistocene; Brazil and western United States.

Neoracanthus, *Essonodontherium* Ameghino. Pleistocene of Argentina.

Zumicrus, *Promegatherium* and *Interodon* Ameghino. Pliocene of Argentina.

Scott considers the *Planopsinae* (*Prepotheriidae* Ameghino), from the Upper Miocene of Santa Cruz in Patagonia, and comprising the genera *Planops* and *Prepotherium* Amegh., to be ancestral to the *Megatheriinae*. These are the largest *Gravigrada* found in the Miocene of Santa Cruz. In common with the *Megatheriinae* they have the massive tail, the elongated ischium and pubis, the short, broad astragalus and a long upper portion of the calcaneum, but lack ridges on the crowns of the teeth.

Subfamily 2. Megalonychinae.

$\frac{5}{4}$ cheek teeth prismatic, quadrangular or transversely elliptical. The first widely separated from the remaining ones, and canine-like. Hindmost tooth small. The

opening of the alveolar canal in front of the base of the coronoid process or on the outer side of the lower jaw, seldom on the inner side.

Megalonyx Jefferson (Fig. 117). Occurs in the Pleistocene and cave deposits of North America, also in the Pliocene (Blanco beds) of Texas. *M. leptostoma* Cope.

Ameghino and Scott have described from the Miocene of Santa Cruz in Patagonia, a number of smaller forms, *Hapalops*, *Eucholoeops*, *Hyperleptus*

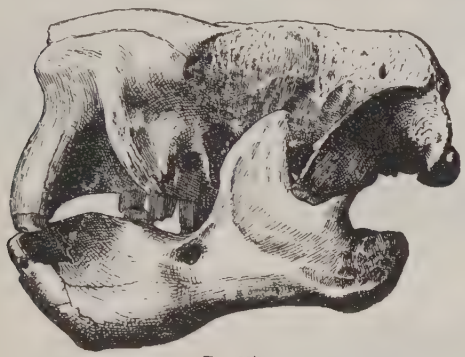


Fig. 117.

*Megalonyx jefferson*i Leidy. Pleistocene of Kentucky. Skull and lower jaw. About 1/6. (After Leidy.)

Fig. 118.

Hyperleptus garzonianus Amegh. Upper Miocene of Santa Cruz, Patagonia. Skull, palatal aspect. 1/3. (After Ameghino.)

(Fig. 118), *Schismotherium*, *Megalonychotherium*, *Analcimorphus* and *Pelecyodon*, etc. Of these *Hapalops* (*Geronops* and *Parahapalops* Ameghino) occurs most abundantly, and comprises the largest number of species; also it is more completely known. All of these genera have a third femoral trochanter and five digits. Still earlier remains are those of *Proplatyarthus* Ameghino from the Astraponotus beds, *Hapalops* from the Pyrotherium beds, and *Hapaloides* and *Proschismotherium* from the Colpodon beds of Patagonia.

Subfamily 3. Mylodontinae.

Cheek teeth prismatic, elliptical-triangular in shape. Last lower M larger than the rest and two-lobed. The posterior branch of the alveolar canal opens on the outer side of the lower jaw.

Mylodon Owen (Fig. 119) $\frac{5}{4}$ *M*, with short snout and rudimentary premaxillary bone. Zygomatic arch incomplete, with a strongly developed descending process. Manus with five digits and pes with four. Dermal ossifications developed to some extent. From the Pleistocene of Argentina, *M. robustus* Owen. In North America, in the Pleistocene of all parts of the United States and in Mexico, *M. harlani* Owen, and *M. garmani* Allen.

Paramylodon Brown. $\frac{4}{4}$ M_3 triangular. Pleistocene of Nebraska and California.

Lestodon Gerv. Jaw broad in front. Pleistocene of Argentina.

Pseudolestodon Gervais and Ameghino. Pleistocene; Tarija Valley, Bolivia.

Scelidotherium Owen. Skull long and low. Muzzle elongated. The manus has four digits, the pes only three. Pleistocene of South America.

Sphenotherus Amegh. (*Platyonyx* Lund). Pleistocene of South America.

Glossotherium Owen (*Neomylodon* Ameghino). The premaxillaries are developed so as to enclose the nostrils in front. *G. listai* Ameghino sp.

FIG. 119.

Mylodon robustus Owen. Pampas formation of Buenos Aires. *A*, Lateral aspect of skull and lower jaw. *B*, Inferior aspect of skull. *C*, Left manus (*R*, radius; *U*, ulna; *s*, scaphoid; *l*, lunare; *c*, cuneiform; *p*, pisiform; *td*, trapezoid; *m*, magnum; *u*, unciform; *I.-V.*, first to fifth digits). *D*, Left pes (*cα*, calcaneum; *a*, astragalus; *n*, navicular; *cb*, cuboid; *c'*, *c''*, cuneiform of II. and III. digits; *II.-V.*, second to fifth digits). All figures 1/6. (After Owen.)

(= *Grypotherium domesticum* Roth) was certainly a contemporary of primitive man. In the cave Eberhardt, on the bay of Ultima Esperanza in Patagonia, numerous remains have been found, among which were fragments of skin containing dermal ossicles.[1]

In the Miocene of Santa Cruz in Patagonia the *Mylodontinae* are not well represented; only a few small forms existing, *Nematherium* (*Ammotherium*, *Limodon*) and *Analcitherium* Ameghino, of which the last named is more closely allied to *Scelidotherium*. In the structure of the skull they are very like the *Megalonychinae* of the same period. In the Lower Tertiary of Patagonia (Pyro-

[1] *Moreno, F. P.*, and *Woodward, A. S.* Proc. Zool. Soc., 1899, p. 144; 1900, p. 64.

therium beds) occur the incompletely known genera *Octodontherium* and *Orophodon* Ameghino.

Tribe 2. HICANODONTA Ameghino.[1]

In all members of this group the endoskeleton is modified for the support of a highly complex exoskeleton in which striking characters of generic importance are present. But the tail sheath, usually made the chief basis of distinction, does not show characters of greater value in classification than any other part of the skeleton.

The tribe is separated at present into four families, the genera of which share many characters in common, chiefly of the exoskeleton. Were the endoskeleton as well known, less difficulty would be experienced in classification. Without doubt the *Glyptodontidae* and *Sclerocalyptidae* include genera that pertain to other families, but they cannot at present be separated.

Family 1. Glyptodontidae.

Glyptodon Owen (Figs. 120, 121). Head truncated, with nasals short and small. Teeth trilobate throughout, with vaso-dentine markedly branched. Humerus without entepicondylar foramen. Manus with four digits.

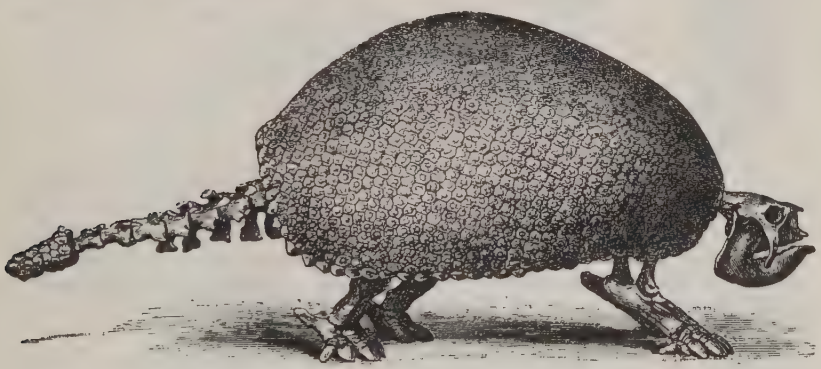


FIG. 120.

Glyptodon reticulatus Owen (=*Schistopleurum typus* Nodot). Pampas formation of Rio Salado, Argentina. Restored skeleton with shell in the Museum at Paris. 1/20. (After Gaudry.)

Pes with five digits. Pubis comparatively small with cross-bars united by cartilage. Head shield plates separate. Carapace large, robust and nearly hemispherical, without anterior lateral prolongation. Caudal sheath short and conical, composed of nine to ten rings with distal plates of each ring large and tuberculate. Pleistocene of Argentina, Bolivia and Brazil.

Glyptotherium Osborn. Pubis greatly reduced, cross-bar vestigial or absent. Carapace medium-sized and elongate, without anterior prolongation. Plates

[1] The descriptions of this group and the arrangement of genera under family divisions are extracted from the most recent classificatory key that has been published on armoured loths, namely that by Barnum Brown as an Appendix to his description of *Brachyostracon*, in Bull. Amer. Mus. Nat. Hist., vol. xxxi., 1912, pp. 167-177.

in transverse rows. Caudal sheath composed of seven movable rings, and a tube of four fused rings, distal rows in each ring slightly elevated. Pliocene of Texas.

Propalaeohoplophorus Ameghino. Premaxillaries with vestigial teeth.

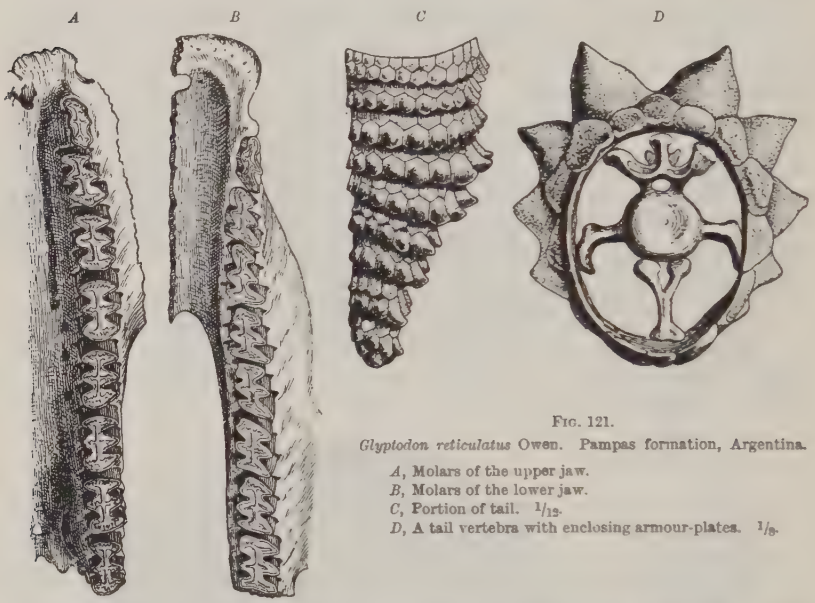


FIG. 121.

Glyptodon reticulatus Owen. Pampas formation, Argentina.

A, Molars of the upper jaw.
B, Molars of the lower jaw.
C, Portion of tail. 1/12.
D, A tail vertebra with enclosing armour-plates. 1/8.

Anterior premolars simple cylinders. Sacrum composed of seven or eight vertebrae. Pubis small, cross-bar small or absent. Manus and pes with five digits. Head shield plates separate. Carapace small, without marked anterior lateral prolongation. Plates in transverse rows. Caudal sheath composed of five or six rings and a terminal tube of two rings closed by a single plate. Miocene of Santa Cruz, Patagonia.

Cochlops Amegh. Skull and teeth similar to *Propalaeohoplophorus*. Head shield plates separate but smaller, thicker and more numerous than in *Propalaeohoplophorus*. Carapace small, plates rough and punctate, with a wide transverse band near the middle, and some over pelvis tuberculate. Miocene of Santa Cruz, Patagonia.

Eucinepeltus Amegh. Head shield composed of eleven to fifteen plates co-ossified, with suture lines raised and no sculptural pattern. Carapace medium-sized with plates marked as in *Propalaeohoplophorus*, but with central figure not elevated and border plates nonserrate. Miocene of Santa Cruz, Patagonia.

Neothoracophorus Amegh. Anterior premolar of lower jaw small and conical. Carapace medium-sized. Plates small, thick and united by tissue, only the central elevated figure surrounded by plane surface. Caudal sheath composed of rings as in *Glyptodon*. Pleistocene of Argentina.

Family 2. Sclerocalyptidae.

Sclerocalyptus Amegh. (*Hoplophorus* Lund) (Fig. 122). Anterior teeth elliptical. Carapace medium-sized, long, straight and cylindrical with anterior lateral prolongation. Manus and pes with four digits. Plates large, with central figure very large and peripheral figures small. Caudal sheath composed of 5 ? anterior movable rings and a long tube ornamented with elliptical figures. Pleistocene of Argentina and Brazil.

Fig. 122.

Sclerocalyptus heusseri Amegh. Pampas formation, Argentina. Tail from the side. 1/6. (After Ameghino.)

Lomaphorus Amegh. First anterior premolars in each jaw cylindrical. Muzzle inflated. Carapace medium-sized and elongate with anterior lateral prolongation. Plates with large round central figure surrounded by single row of polygonal figures. Caudal sheath composed of three or four rings, terminal tube short and wide. Pleistocene of Argentina.

Panochthus Burm. (Figs. 123, 124). First lower premolar an elongate ellipse, perpendicular angles present. Manus with three, and pes with four digits.

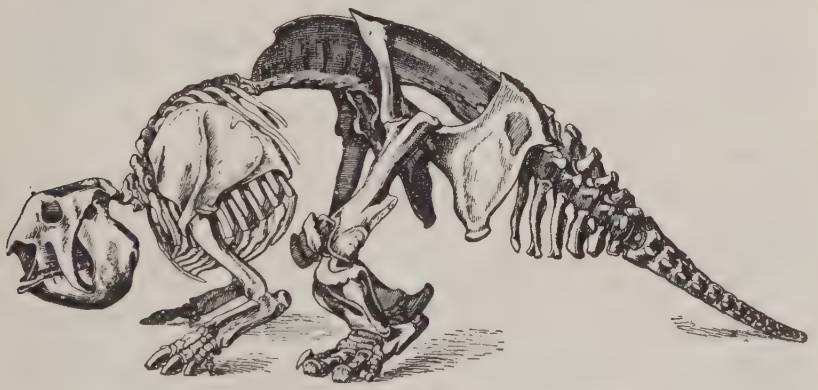


Fig. 123.

Panochthus tuberculatus Owen sp. Pampas formation, Argentina. Restored skeleton without shell. 1/22. (After Burmeister.)

Carapace largest of order, an elongate oval with anterior lateral prolongation. Dorsal region raised above pelvis in a hump. Plates marked by polygonal figures of equal size and complete; central figure sometimes present. Caudal sheath with six rings and a long flattened tube ornamented with tubercles. Pleistocene of Argentina.

Palaeohoplophorus Amegh. Carapace medium-sized. Plates with large central figure surrounded by two lines and a third incomplete line of peripheral figures. Caudal sheath with 2 ? movable rings and a conical elliptical tube as in *Sclerocalyptus*. Pliocene of Argentina.

Brachyostracon Brown. Two anterior lower premolars elliptical, vasodentine ridges feebly branched; sacrum composed of sixteen vertebrae, four

united with ilia and two united with ischia. Pubis large and cross-bar massive. Carapace large and elliptical; a prominent median hump divides it into a short posterior recurved and a long anterior decurved end. Plates of carapace inside of border with round central figure surrounded by single row of eight to twelve peripheral figures. Pleistocene; Mexico.

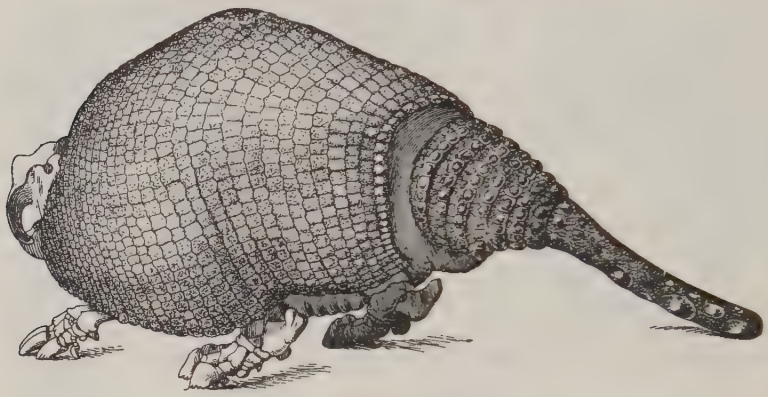


FIG. 124.

Panochthus tuberculatus Owen sp. Pampas formation of the Province of Buenos Aires. Shell restored. 1/20. (After Burmeister.)

Family 3. **Doedicuridae.**

Neuryurus Amegh. Anterior premolars small and elliptical. Carapace medium to large size. Plates of carapace small and disposed in transverse rows; surface elevated in centre and pitted, without figures. Caudal sheath ending in long depressed tube, composed of plates similar to those of carapace excepting on lateral face, where plates are elliptical and large. Pliocene of Argentina and Pleistocene of Brazil.

Doedicurus Amegh. Head convex as in *Panochthus*, and orbit completely enclosed by bony ring. First premolars smaller than succeeding teeth and semi-elliptical. Humerus with entepicondylar foramen. Manus with three functional digits. Pes with four digits. Head shield formed of small plates not suturally united. Carapace large, with anterior lateral prolongation. Plates polygonal, no figures, pitted, and convex or plane with three or five large openings on surface. Caudal sheath a large tube, very long, depressed and thickened transversely at the end, where it is ornamented with large spines. Pleistocene of Argentina and Uruguay.

Family 4. **Dasypodidae.** Armadillos.

Armour composed either entirely of movable transverse rows of bony plates, or of consolidated pectoral and pelvic shields with movable rings lying between. Skull long, low with slender muzzle. Zygomatic arch without downwardly directed process. Teeth $\left(\begin{matrix}8\text{-}9\\9\text{-}10\end{matrix}\right)$ *prismatic, frequently heterodont. All dorsal and lumbar vertebrae*

free. Humerus with entepicondylar foramen; femur with third trochanter. Extremities pentadactyl.

The *Dasypodidae* are distinguished from the *Glyptodontidae* by their more primitive structure, such as their movable armour, elongated skull, simple teeth, lack of marginal plates and free vertebrae. In size they fall far short of the *Glyptodontidae*, with the single exception of *Chlamydotherium*.

Armadillos at the present day inhabit tropical and temperate South America, only one genus, *Tatusia*, extending from Central America into Mexico and Texas. Fossil *Dasypodidae* have been found only in South America. A fragment of bony armour, described by Filhol from the Quercy Phosphorites under the name of *Necromanis galliae*, and theoretically associated by Ameghino with the skull of *Necromanis edwardsi* Filhol, belongs to the Eocene lizard *Placosaurus*. The reduced dentition $\frac{0.1.1.}{1.1.2.}$ $\left(\text{functionally } \frac{0.1.0.}{0.1.0.}\right)$ of *Metachiromys* Wortman, from the Bridger Eocene of Wyoming, does not agree with Osborn's theory, that these remains belong to an armadillo lacking armour.

FIG. 125.

Prozaëdius proximus Amegh. Miocene of Santa Cruz. Armour-plates. $^1/_1$.

FIG. 126.

Stegotherium tessellatum Amegh. Miocene of Santa Cruz. Skull. $^1/_2$. (After Scott.)

The *Dasypodidae* from the Pleistocene of South America, Pampas formation of Argentina and from the Brazilian bone caves, belong for the most part to recent genera—*Tatusia*, *Dasypus*, *Tolypeutes*, *Xenurus*, etc. *Chlamydotherium* Lund is distinguished by attaining huge size even as early as the Pliocene, when it occurs together with *Proeuphractus* and *Eutatus* Amegh.

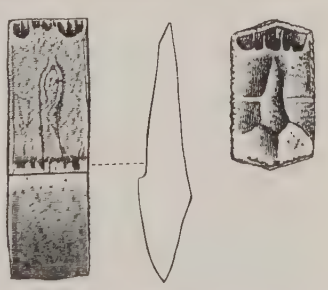


FIG. 127.

Meteutatus lagenaeformis Amegh. Pyrotherium strata of Lower Miocene, Patagonia. Armour-plates. $^1/_1$.

Very complete remains are described by Scott from the Miocene of Santa Cruz in Patagonia. The genera which have been made known from this region are *Proeutatus*, *Prozaëdius* (Fig. 125), *Stenotatus* Amegh., *Pareutatus* Scott, and *Stegotherium* and *Peltephilus* Amegh., of which the latter two are of especial interest. *Stegotherium* (Fig. 126) is related to the *Myrmecophagidae*, on account of its elongated snout, and much-reduced teeth, which are restricted to the posterior region of the jaw. *Peltephilus* has a short, broad muzzle and a broad casque, composed of but a few bony plates, and among these there are

two with well-developed horns. These genera are found also in the Colpodon beds with a few forms in the Pyrotherium beds, which are very similar to some from the Eocene Notostylops beds. The genera *Prostegotherium*, *Utaetus*, *Meteutatus* (Fig. 127), *Machiydotherium* Amegh., etc., include some of the oldest known remains of fossil armadillos.

Order VI. RODENTIA. Glires (Rodents).[1]

Extremities with claws, seldom with hoof-like nails. Dentition with $\frac{1}{1}$ *I, less frequently with* $\frac{2}{1}$ *I. I very long, with persistent pulp, usually covered with enamel on only the anterior and outer surfaces, and with sharp, chisel-like gnawing surfaces. Cheek teeth* $\frac{2\text{-}6}{2\text{-}6}$ *separated from the incisors by a long diastema, brachyodont, bunodont, lophodont or prismatic. Articular condyle of the mandible fitting into a groove and capable of antero-posterior motion.*

The rodents form a homogeneous, very sharply defined order of Placentals, possibly derived from primitive Insectivores, certain forms of which have a highly specialised dentition. They are for the most part small burrowing herbivorous animals, and are sometimes also adapted for climbing and swimming. The dentition and skeleton are greatly modified in adaptation to subsistence and life habits.

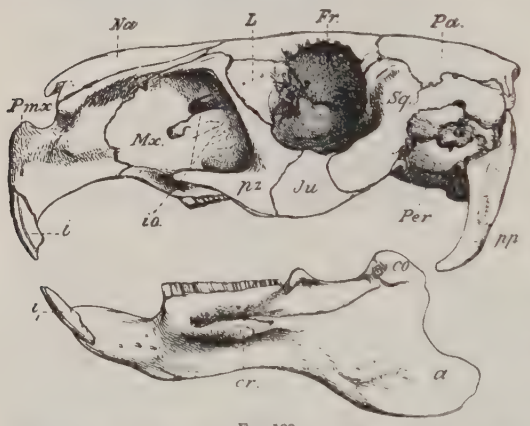


Fig. 128.

Hydrochoerus capybara Erx!. South America. Skull and lower jaw. 1/2 (after Flower). *Pmx*, Premaxilla; *Mx*, maxilla; *Na*, nasal; *L*, lachrymal; *Fr*, frontal; *Pa*, parietal; *Sq*, squamosal; *Ju*, jugal; *Per*, periotic; *i*, upper incisor; i_1, lower incisor; *io*, infraorbital canal; *pz*, zygomatic process of the upper jaw; *pp*, paroccipital process; *co*, condyle; *a*, angle; *cr*, masseter crest of the mandible.

The skull (Fig. 128) is for the most part low, the muzzle long, and the posterior portion of the head very abruptly truncated. The smooth cerebral hemispheres are of moderate size, the cerebellum and olfactory lobes relatively large. The nasal region is capacious and filled by the turbinate bones. The nostrils always anteriorly placed. The paroccipital process is frequently very long. The orbits are open

[1] *Brandt, J. F.* Mém. Acad. Imp. Sci. St. Pétersb., 1835, 6 sér., vol. iii., pp. 77-336.—*Cope, E. D.*, The extinct Rodentia of North America. Amer. Naturalist, 1883, p. 43; 165; 370.—*Forsyth Major, C. J.*, Nageruberreste aus Bohnerzen Süd-Deutschlands und der Schweiz. Palaeontogr., 1873, vol. xxii.—On fossil and recent Lagomorpha. Trans. Linn. Soc. London, 1899.—*Matthew, W. D.* Bull. Amer. Mus. Nat. Hist., New York, 1902, art. xxii.; 1910, art. vi.—*Nehring, A.*, Beitrag zur Kenntnis der Diluvialfauna (Nager). Zeitschr. für Ges. Naturw., 1876, xlvii. and xlviii.—*Peterson, O. A.*, New Rodents and Discussion of *Ischyromys*. Mem. Carnegie Mus., Pittsburgh, 1905, vol. ii. No. 4.—*Schlosser, M.*, Nager des europäischen Tertiärs. Palaeontogr., 1884, vol. xxxi.—*Scott, W. B.*, Report of the Princeton Univers. Exped. to Patagonia, 1905, vol. v. part iii.—*Tullberg, T.*, System der Nagetiere. Nova Acta Soc. Scienc. Upsala, 1899.—*Winge, H.*, Jordfundne og nu levende Gnavere (Rodentia) fra brasilien. E Museo Lundii Kjøbenhaven, 1888.

posteriorly. The strong zygomatic arch is perforated by the infraorbital foramen, which frequently forms so broad a channel that not only the nervus facialis but also a portion of the masseter muscle passes through it. In the *Hystricoidea* and *Anomaluroidea* the size of this opening is so great that it exceeds the orbit. The jugal is always well developed, and the lachrymal is considerably expanded. The anterior palatal foramina are of considerable size. The lower jaw often has a prominent crest for the attachment of the masseter muscle. The condyle is rounded oval, not transversely extended, and is set high up on the jaw.

A clavicular element is frequently present in the shoulder girdle. The bones of the forearm are, as a rule, capable of free supination. A centrale is often present in the carpus. Scaphoid and lunar are frequently fused. The first of the five digits is often less developed than the rest. The pointed terminal phalanges are clawed.

In the pelvic girdle the ilium is remarkable for its slender, triangular form, the pubes and ischia are large, and the two pubic bones are united in the median line to form a long symphysis. The femur often bears a third trochanter. The fibula and tibia are not infrequently fused at their distal extremities, but all of the tarsals remain distinct. The digits are often five in number—rarely three, and in the latter case a fusion of the metatarsals is often observed.

In contra-distinction to the primitive structure of the skull and of the skeleton, the dentition, even of the oldest known rodents, is very highly specialised. The dental formula varies between $\frac{2.0.3.3.}{1.0.3.2.}$ and $\frac{1.0.2.}{1.0.2.}$. The canines have entirely disappeared, and the cheek teeth are separated by a long diastema from the incisors, of which there is, as a rule, only one in each jaw, and that is the original I_2. Only in the suborder *Duplicidentata* is there a small I^3 behind the large I^2. The incisors, called in this order gnawing teeth, on account of their function, continue to grow as their crown is worn down through use. The cheek teeth are never complete in number. The premolars may be entirely lacking and the last of the molars may be very small. With the exception of the first P all the cheek teeth have similar construction. They are short, brachyodont and rooted in some forms, and high, hypsodont, prismatic and open below, even in old age being without roots, in others. The former have bunodont or lophodont crowns, the latter consist of prisms or cylinders with patches of enamel on their crowns, at times—the remnant of former transverse ridges—or of compressed lamellae. Originally the upper cheek teeth had three or four cusps and the lower ones four, with a crested anterior and posterior border. Later the neighbouring cusps united to form ridges. Since the enamel covering is worn down on the ridges of the crowns through use, the enamel is often lacking in these parts even in the young tooth. The valleys in the tooth thus form the enamel inflections or fossettes, which disappear partly or wholly with further wear.

The change in dentition is restricted in the rodents, as a rule, to the P; the I are renewed only in *Duplicidentata*. In the rodents which have four cheek teeth, the three hind ones are M and the front one a P, which has often no milk predecessor. In most cases, however, a milk tooth, D, precedes

this *P*, and in the geologically older rodents it is more complicated, and functions for a greater length of time, than in the more recent forms, where the replacement often occurs in the foetus, as in the case of *Caviinae*. In the embryo of *Sciurus* Adloff has seen traces of the formation of three incisors and one canine.

Rodents at the present day exceed all other mammalian orders in number of genera and species. More than 900 living species have been counted, of which a large portion inhabit South America. North America and Eurasia have many genera in common. In Africa, in addition to a number of peculiar types, are found representatives of European and Asiatic families and genera.

In spite of their small size and delicate structure the number of fossil remains of rodents is considerable. In Europe quite a number of species from the Upper Eocene and Oligocene are known, especially from the Phosphorites of Quercy and from the Miocene deposits in the Department of Allier, those of Mayence and Ulm, as well as of Sansan (Dept. Gers), La Grive St. Alban (Dept. Isère), of Steinheim and from the Ries near Nördlingen. In North America the rodents are less abundant, and are found chiefly in the Bridger Eocene, in the White River Oligocene, and in the John Day and Loup Fork Miocene. South America, on the other hand, possesses an abundant rodent fauna, found in the Santa Cruz formation of Patagonia and in the early Tertiary and Pleistocene of Argentina. Rodent remains have been discovered also in several Pleistocene cave deposits of Europe, North and South America.

The classification of the rodents offers many difficulties, for though the two suborders *Duplicidentata* and *Simplicidentata* are well defined, yet the arrangement of certain forms of the latter group under the three principal subdivisions employed up to the present time, namely, *Sciuromorpha*, *Myomorpha* and *Hystricomorpha*, is very difficult. The formation of a fourth subdivision, *Protrogomorpha*, is only a makeshift, which would serve to confuse the relationship between many fossil forms and their living representatives, as would also the proposed plan of Tullberg, to divide all the forms into the two tribes *Sciurognathi* and *Hystricognathi*. The most feasible plan of classification seems to be that of Weber, which has been adopted here with several additions.

Suborder A. SIMPLICIDENTATA.

There is always only $\frac{1}{1}$ *long incisor. Premolars* $\frac{2}{1}$, *more frequently* $\frac{1}{1}$, *often* $\frac{0}{0}$. *Enamel on the incisor is almost always yellow and restricted to the front surface of the tooth. The dentition of the upper jaw is more compact than that of the lower. The articulation for the lower jaw is narrow. Scaphoid and lunar are mostly fused. Fibula not articulating with the calcaneum.*

Family 1. Aplodontoidea Gill.

$\frac{2}{1}$ *P.* $\frac{3}{3}$ *M. Cranial roof flat. Masseter not extending through or beyond the small infraorbital foramen. No postorbital process. Tibia and fibula not fused.*

Subfamily 1. Aplodontiinae Thomas.

Cheek teeth, as a rule, brachyodont. In place of the cusps they have irregular, non-parallel ridges.

Sciurodon Schlosser. Phosphorites of Quercy.

Meniscomys Cope (*Allomys* Marsh). Lower Miocene. John Day beds; Oregon.

Mylagaulodon Sinclair. Lower Miocene; Montana.

Haplodon Rafin. Hypsodont. Recent, Pliocene and Pleistocene of North America.

Subfamily 2. Ischyromyinae Alston.

Cheek teeth brachyodont. Eocene and Oligocene of North America.

Ischyromys Leidy (Fig. 129). Both pairs of cusps of the upper *M* are opposite, of the lower *M* they are alternating. Oligocene. White River beds.

Mysops Leidy (*Tillomys* Marsh). Eocene. Bridger beds.

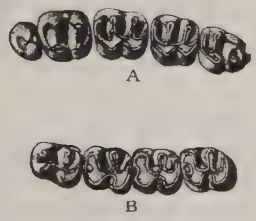


Fig. 129.

Ischyromys typus Leidy. Oligocene of White River beds. *A*, Upper and *B*, lower tooth-row. $^3/_1$.

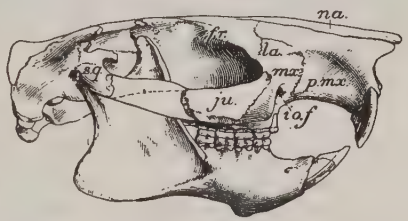


Fig. 130.

Paramys delicatus Leidy. Middle Eocene. Bridger beds of Wyoming. Skull and lower jaw. $^1/_2$. (After Matthew.)

Titanotheriomys Matthew. Lower Oligocene. Titanotherium beds.

Paramys Leidy (*Pseudotomus* Cope) (Fig. 130). Upper *M* tritubercular, the second pair of cusps of the lower *M* form the posterior border of the tooth, as is practically the case also in *Sciurus*. Many different species in the Eocene of North America. Also Lower Eocene of France.

Plesiarctomys Bravard. Eocene. Débruge.

Sciuravus Marsh. Upper *M* with four tubercles. Eocene of North America.

Family 2. **Sciuroidea.**

$\frac{2}{1}$ *P.* $\frac{3}{3}$ *M. Skull arched. Infraorbital canal small. The anterior branch of the masseter is attached on the front side of the zygomatic arch. Postorbital process present. Tibia and fibula not fused.*

Subfamily. Sciurinae.

Cheek teeth are brachyodont, bunodont or lophodont. The second pair of cusps of the lower cheek teeth form the posterior surface. Upper M and P^4 *tritubercular.*

The *Sciurinae* may be derived from *Paramys*, and have a world-wide distribution.

Plesiospermophilus Filhol. Phosphorites of Quercy.

Spermophilus Cuvier. Pouched marmots. Recent in the northern hemisphere. Fossil in the Pleistocene.

Prosciurus Matthew. White River Oligocene and John Day Miocene. Transition between *Paramys* and *Sciurus*.

Arctomys Gmelin. Marmot. Fossil in the European and North American Pleistocene.

Cynomys Rafinesque. North America. Fossil in the Upper Miocene and onward.

Sciurus Linn. Squirrel. Fossil in Europe and North America in the Miocene and Pleistocene.

Tamias Illiger. Recent and in the Pleistocene of North America.

Sciuropterus Cuvier. Flying squirrels. Recent in Asia and in the north part of Europe and North America. Upper Miocene of Germany.

Pteromys Cuvier. Lophodont. Recent in Southern Asia.

Family 3. Castoroidea.

$\frac{1}{1}$ *P.* $\frac{3\text{-}2}{3\text{-}2}$ *M. Cranial roof flat, mostly without postorbital process. Infraorbital foramen small. Cheek teeth with enamel folded into ridges and valleys, more or less hypsodont.*

Subfamily 1. Castorinae. Beavers.

Skull low. $\frac{3}{3}$ *M. Cheek teeth more or less hypsodont. Upper teeth usually with three outer and one inner fold, lower with three inner and one outer fold. These folds are either transverse or parallel to the dental row. Tibia and fibula fused distally.* Recent in Europe and North America; fossil forms ranging from the Oligocene in the latter and from the Miocene in the former.

Steneofiber Geoffroy (*Chalicomys, Chelodus* Kaup; *Palaeocastor* Leidy) (Figs. 131, 132). Many species in the Miocene of North America, often in the

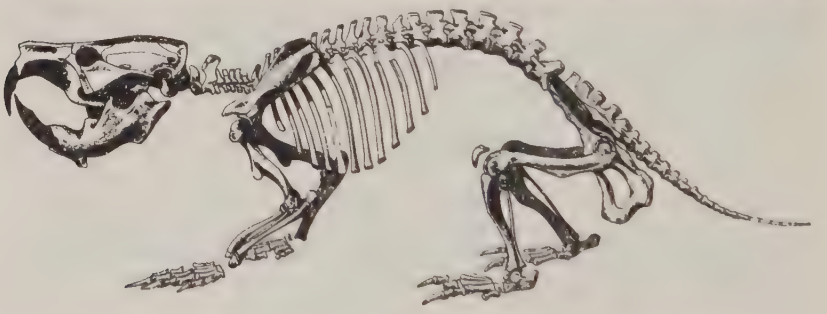


Fig. 131.

Steneofiber fossor Peterson. Upper Miocene, Sioux Co., Nebraska. Skeleton. 1/8. (After Peterson.)

Reproduced, by permission, from The Memoirs of the Carnegie Museum.

European Miocene, less frequently in the Pliocene. The American forms have a broad skull. The subterranean burrows are named *Daemonelix*.

Euhapsis Peterson. Lower Miocene; North America.

Castor Linn. Beaver (Fig. 133). Teeth very hypsodont. Recent in Europe and North America. Fossil in Europe in the Pliocene and Pleistocene, and in North America in the Pleistocene.

Fig. 132.

Steneofiber eseri H. v. Meyer (=*St. viciacensis* Gervais). Lower Miocene of St. Gérand-le-Puy, Allier. Lower aspect of skull. 3/4. (After Filhol.)

Trogontherium Fischer. Lower Pleistocene of Europe.

Castoroides Forster. About the size of a bear. Pleistocene of North America.

Eucastor Leidy (*Sigmogomphius* Merriam). Miocene of North America. *Dipoides* Jäger, in the Pliocene of Europe, China, and in the Miocene of North America. These are distinguished by a small number of enamel folds.

Fig. 133.

Longitudinal vertical section through the skull of a beaver (*Castor fiber* Linn.) to show the roots of the incisor and the molars. (After Flower.)

Eutypomys Matthew has two upper *P.* Cheek teeth with many small enamel fossettes. Oligocene (White River beds).

Subfamily 2. Mylagaulinae.

Skull very broad with postorbital process. Cheek teeth high, with many enamel fossettes elongated mostly parallel to the jaw. Extremities stout, adapted for digging. Tibia and fibula free. In the Miocene and Lower Pliocene of North America. According to Riggs these are the descendants of *Meniscomys.*

Mylagaulus Cope; *Mesogaulus* Riggs; *Ceratogaulus* Matthew (with bony horn-core on the nasals); *Epigaulus* Gidley.

Family 4. Geomyoidea.

$\frac{1}{1}$ *P.* $\frac{3}{3}$ *M. Skull usually with small infraorbital foramen, without postorbital process, with large ossified bulla. Cheek teeth mostly hypsodont with one fold through the centre of the tooth. Tibia fused with fibula.* Only in North America.

Subfamily 1. Protoptychinae.

Infraorbital canal large. Teeth with roots.

Protoptychus Scott. Upper Eocene (Uinta beds); North America.

Subfamily 2. Geomyinae.

Infraorbital foramen small. Cheek teeth without roots, with outer and inner folds or sometimes with only one transverse fold.

Entoptychus Cope (Fig. 134) and *Pleurolicus* Cope. Lower Miocene of North America.

Geomys Raf. Molars are simple prisms. In the Miocene, Pleistocene and Recent of North America.

Thomomys Wied. Miocene, Pliocene, Pleistocene and Recent in North America.

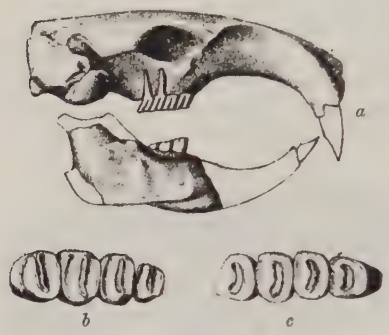


Fig. 134.

Entoptychus planifrons Cope. *a*, Skull and lower jaw, $^1/_1$ (after Cope); *b*, upper and *c*, lower tooth-row, $^3/_1$. Lower Miocene of John Day beds, Oregon.

Family 5. Anomaluroidea.

$\frac{1}{1}$ *P.* $\frac{3}{3}$ *M. Cheek teeth brachyodont, bunodont or lophodont. Infraorbital foramen large. Tibia and fibula articulate freely.* The Recent subfamilies, restricted to Africa, *Anomalurinae* and *Pedetinae*, are not known as fossils. The fossil forms here referred to the *Anomaluroidea* possibly bear only an accidental similarity.

Subfamily 1. Pseudosciurinae.

Cheek teeth bunodont. Cusps grouped in pairs. D smaller than P.

Sciuroides F. Major. Pairs of cusps of the cheek teeth are joined to form ridges. Upper *M* with insignificant cusps lying between these ridges. Eocene and Oligocene. In the Bohnerz of Switzerland and Würtemberg, also in the Phosphorites of Quercy.

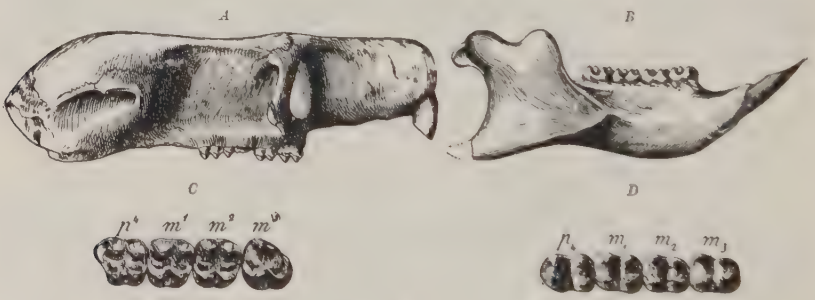


Fig. 135.

Pseudosciurus suevicus Hensel. Oligocene (Bohnerz) of Eselsberg near Ulm. *A*, Skull. *B*, Exterior aspect of mandible, $^1/_1$. *C*, Upper and *D*, lower tooth-row (enlarged).

Pseudosciurus Hensel (Fig 135). Cusps isolated. Upper *M* with distinct intermediate cusps. Bohnerz of Würtemberg.

Subfamily 2. THERIDOMYINAE.

Cheek teeth lophodont. Cusps recognisable only in the oldest forms, being worn down in later forms, with three to four outer folds and one inner fold on the upper teeth, and three to four inner and one or two outer folds on the lower teeth. D usually more complicated than P. Tibia and fibula free. In the Eocene, Oligocene and Miocene of Europe.

This subfamily has a common origin with the foregoing, and is the ancestor of certain *Hystricoidea—Capromyinae, Erethizontinae, Octodontinae, Chinchillinae* and *Echinomyinae.*

Theridomys Jourdan (Fig. 136). *P* always larger than *M.* Eocene; Débruge, Vaucluse. Swabian and Swiss Bohnerz. Oligocene Phosphorites, and Ronzon.

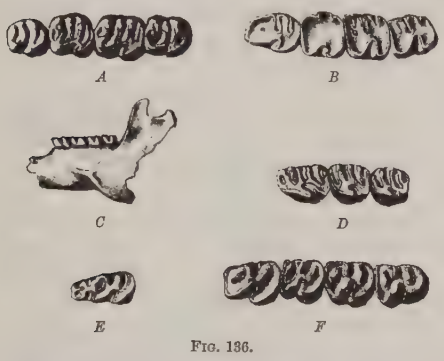


FIG. 136.

A and *B*, Upper and lower tooth-row of *Theridomys vaillanti* Gervais. $^3/_1$. Upper Eocene of Débruge (Vaucluse). *C*, *D*, *E* and *F*, *Theridomys gregarius* Schlosser. Oligocene (Phosphorite) of Quercy. *C*, Lower jaw; *D*, upper tooth-row with D_4; *E*, lower D_4; *F*, lower tooth-row with P_4. $^3/_1$.

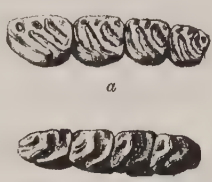


FIG. 137.

Protechimys major Schlosser. Oligocene (Phosphorite) of Quercy. *a*, Upper and *b*, lower tooth-row. $^3/_1$.

Trechomys Lartet. *P* usually much smaller than *M.* *D* simple. Eocene; Paris. Phosphorites of Quercy.

Phiomys Osborn. Middle transverse ridge short. Oligocene; Egypt.

Protechimys Schlosser (Fig. 137). Folds oblique. Cheek teeth cleft on account of the fusion of the outer and inner folds. Crowns somewhat hypsodont. Phosphorites of Quercy.

Archaeomys Laiz. et Parieu. Similar to the last. Crowns of the teeth rather hypsodont. Oligocene; Dept. Allier, France.

Rhodanomys Depéret. Lower Miocene of Savoy and Ulm.

Family 6. **Myoxoidea.** Dormice.

$\frac{1\text{-}0}{1\text{-}0}$ *P.* $\frac{3}{3}$ *M. Cheek teeth always brachyodont with parallel or converging enamel ridges. Infraorbital canal large and in an elevated position. Tibia and fibula fused.* Recent in the Palaearctic and Ethiopian regions.

Of the species having four cheek teeth, almost all were represented in the European Tertiary.

Myoxus Schreber (Fig. 138 *A*). Probably already in the Eocene (Phosphorites, Paris gypsum ?), but definitely known from the Miocene.

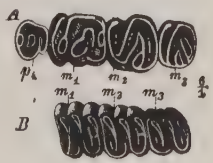


FIG. 138.

A, *Myoxus sansaniensis* Lartet. Upper Miocene of Ries. Upper molars. $^6/_1$.

B, *Eliomys hamadryas* F. Major. Upper Miocene of Steinheim. Lower molars. $^6/_1$.

Eliomys Wagner (Fig. 138 *B*). Miocene. *Muscardinus* Wagner. Fossil in the Pleistocene.

Leithia Lydekker. Pleistocene of Malta.

Family 7. **Dipodoidea.** Jumping Mice.

$\frac{1}{1}$, $\frac{1}{0}$ *or* $\frac{0}{0}$ *P.* $\frac{3}{3}$ *M. Cheek teeth brachyodont, usually rooted, with alternating cusps. Infraorbital canal large and round. Fibula and tibia fused. Hind-limb elongated, metatarsals often fused.*

The jumping mice inhabit at present the deserts and steppes of the northern hemisphere. The fossil remains belong to living genera and species, and are only known from the European Pleistocene.

The *Zapodinae* have five free metatarsals. *Sminthus* Keys. Also fossil in Europe.

The three middle metatarsals of the *Dipodinae* are very much elongated and fused throughout their complete length.

Alactaga Cuvier. Pes three-toed. Pleistocene of Europe.

Dipus Gmelin. Pes five-toed.

Sciuromys Schlosser. $\frac{1}{1}$ *P.* $\frac{3}{3}$ *M.* Teeth similar to those of *Alactaga*. Phosphorites of Quercy. Systematic position uncertain.

Family 8. **Myoidea** (*Myomorpha*).

($?\ \frac{1}{1}$ *P*) $\frac{3\text{-}2}{3\text{-}2}$ *M. Infraorbital foramen large. Zygomatic arch small. Cheek teeth brachyodont, bunodont or lophodont or else hypsodont, prismatic. First M, as a rule, large and more complicated than* M_2 *and* M_3. *Lower jaw with high coronoid process. Angle of the lower jaw arising from the inferior surface of the incisor alveolus. Fibula fused with the tibia.*

The *Myoidea* are usually small, and are at present dispersed over the entire earth's surface.

Subfamily 1. Eomyinae.

$\frac{1}{1}$ *P.* $\frac{3}{3}$ *M. Cheek teeth brachyodont, with two opposing pairs of cusps, and considerable front and hind surface and ridge running along the centre of the tooth.* Oligocene of Europe and North America.

These small rodents are placed by Winge under the *Dipodoidea* and by Scott under the *Geomyidae*. The dental arrangement, as in *Cricetodon*, makes it possible for these forms to be considered as primitive *Murinae*.

Eomys Schlosser. Phosphorites of Quercy.

Gymnoptychus Leidy. Skull as in *Geomyinae*, but teeth brachyodont. Oligocene (White River beds).

Subfamily 2. Cricetinae. Hamsters.

$\frac{3}{3}$ *M. Cheek teeth bunodont, rooted, with four paired regularly arranged cusps.* M_1 *with five or six tubercles.*

The *Cricetinae* inhabit the northern hemisphere.

Cricetodon Lartet (Fig. 139). *M* with five tubercles. Eocene Bohnerz; Oligocene Phosphorites; Ronzon. Lower and Upper Miocene of Europe.

Eumys Leidy. Oligocene. White River beds.

Cricetus Pallas. M_1 with six cusps. Recent and fossil in the Pleistocene of Europe. Pliocene of Roussillon.

Subfamily 3. Hesperomyinae.

$\frac{3}{3}$ *M. Dentition similar to that of the Cricetinae.* Recent in North and South America.

Hesperomys Waterhouse (Fig. 140). Recent and in the Pliocene and Pleistocene of South America.

Neotoma Say. Recent and in the Pleistocene of North America.

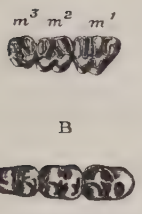


Fig. 139.

Cricetodon cadurcensis Schlosser. Phosphorite near Mouillac, Tarn-et-Garonne. *A*, Upper molars greatly worn down. $^3/_1$ (after Schlosser). *B*, Lower molars. $^4/_1$.

Fig. 140.

Hesperomys molitor Winge. Cave of Escrivania, Brazil. Inferior and superior aspect of skull. $^1/_1$. (After Winge.)

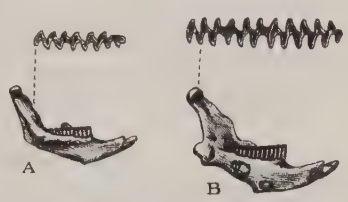


Fig. 141.

A, Arvicola arvalis Blasius. *B, Cuniculus torquatus* Pallas sp. Pleistocene of Velburg. Interior aspect of mandible and superior aspect of lower molars (enlarged).

Paciculus Cope. *Peromyscus* Glover. In the Lower Miocene of Oregon.

Habrothrix, Oxymycterus, Colomys, etc. Recent and in the Pleistocene of South America.

Subfamily 4. Murinae. Rats and Mice.

$\frac{3}{3}$ *M. Cheek teeth brachyodont and with roots, upper with three, lower with two rows of tubercles.*

The *Murinae* are animals of the Old World, but have spread over the entire globe. Fossil remains have been found in small numbers in the European Pliocene and Pleistocene. Asia and Africa have yielded several fossil forms also, which belong to the genera *Mus, Gerbillus* and *Nesokia.*

Mus Linn. First appears in the Pliocene of Roussillon. *Acomys* Geoffroy. Fossil in the Lower Pliocene of Pikermi. In the Miocene of La Grive St. Alban is found a Nesomyine, *Anomalomys* Gaillard.

Subfamily 5. Arvicolinae. Voles.

$\frac{3}{3}$ *M. Cheek teeth prismatic, made up of two longitudinal rows of three to six angular prisms more or less distinct.* Recent in Europe and the northern part of Asia and North America.

Arvicola Lacépède (*Hypudaeus* Illiger) (Fig. 141 *A*). Posterior extremity of the incisor extending behind the last *M*. Many Recent forms found also in the Pleistocene of Europe.

Cuniculus Wagner (Banded lemming) (Figs. 141 *B*, 142). Posterior extremity of the incisor terminating below the last *M*. Recent in northern Europe. Fossil in the Pleistocene.

FIG. 142.

Cuniculus torquatus Pall. sp. Pleistocene of Velburg. Lower *P*. $^3/_1$.

Myodes Pallas (*Lemmus* Linck). Same locality and horizon as the preceding.

Microtus Schrank. *Fiber* Cuvier. Recent and in the Pleistocene of North America. *Anaptogonia*, *Sycium* Cope. Pleistocene of North America. *Mimomys* F. Major. Teeth with roots, rather high. Pliocene of Norwich. *Ruscinomys* Depéret. Pliocene of Roussillon. *Lophiomys* Depéret from the same locality. Systematic position doubtful.

Subfamily 6. SPALACINAE.

Skull and dental formula similar to that of the Dipodinae.

Siphneus Brants. Recent and fossil in northern Asia. *Rhizomys* Gray. Recent in Asia, fossil in the Pliocene of Siwalik.

Prospalax Kormos. Fossil in the Pliocene and Pleistocene of Hungary.

Family 9. **Hystricoidea** (*Hystricomorpha*).

Angle of the mandible arising from the lateral surface of the incisor alveolus. Coronoid process low, jaws movable only in an antero-posterior direction. Skull flat, without postorbital process and with very wide infraorbital canal. $\frac{1.0.1.3.}{1.0.1.3.}$ *Cheek teeth with enamel folds, usually prismatic-hypsodont, seldom brachyodont. Fibula free.*

The *Hystricoidea* appear first as *Hystricinae*, *Theridomyinae* and *Issiodoromyinae* in Europe. The *Hystricinae* spread later over the entire surface of the eastern hemisphere; the two remaining subfamilies wander to South America, and develop in that region as *Erethizontinae*, *Capromyinae*, *Chinchillinae*, *Octodontinae* and *Caviinae*. The *Ctenodactylinae* and *Bathyergidae* are restricted to Africa, and are not yet known to exist as fossils.

Subfamily 1. HYSTRICINAE. Old World Porcupines.

Cheek teeth with roots, moderately hypsodont. Crowns with enamel folds and fossettes.

Hystrix Linn. Fossil in Europe from the Oligocene through the Pleistocene. In the Pliocene and Pleistocene also in India. A large well-known form from the Eocene of Quercy is "*Hystrix*" *lamandini* Filhol.

Subfamily 2. ERETHIZONTINAE. New World Porcupines.

Cheek teeth brachyodont. Descendants of *Trechomys*?

Eosteiromys Amegh. Colpodon strata of Patagonia. *Steiromys* Ameghino in the Miocene of Santa Cruz.

Coendu Lacép. Recent in South America. Fossil in the bone caverns of Brazil.

Erethizon F. Cuvier. Recent and in the Pleistocene of North America.

Sciamys and *Acaremys* Amegh. (Fig. 143) in the Miocene of Santa Cruz and *Protacaremys* Amegh. in the Colpodon beds of Patagonia, are small forms.

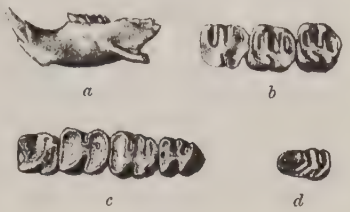


FIG. 143.

Acaremys messor Amegh. Upper Miocene of Santa Cruz, Patagonia. *a*, Mandible, $^1/_1$; *b*, upper tooth-row without M_3; *c*, lower tooth-row; *d*, lower D_4, $^3/_1$.

Subfamily 3. CAPROMYINAE.

Teeth shaped like those of Castoridae. Usually moderate-sized forms. Descendants of *Theridomys*?

Myocastor Kerr (*Myopotamus* Geoffr.). Recent in South America. Fossil in the Pliocene.

Morenia, *Discolomys* Ameghino. Pliocene of Argentina.

Neoreomys Ameghino, in the Santa Cruz formation of Patagonia. The genera *Scleromys* and *Lomomys* Ameghino are from the same locality.

Subfamily 4. OCTODONTINAE.

The group of *Octodontinae* arises in the Pliocene of Argentina with *Dicoelophorus* and *Plataeomys* of Ameghino. *Ctenomys* Blv. first appears in the Pleistocene of South America. The group of *Loncherinae* has representatives in the early Miocene of Patagonia (Colpodon beds), such as *Protadelphomys* and *Prospaniomys*. In the Miocene of Santa Cruz are found *Stichomys*, *Adelphomys*, *Spaniomys* (Fig. 144), etc., of Ameghino. *Loncheres* Illiger, *Echinomys* and *Mesomys* Desm. are known from fossil remains in Brazilian caves.

FIG. 144.

Spaniomys modestus Amegh. *a*, Upper tooth-row; *b*, lower tooth-row with exception of *M.* $^3/_1$. Upper Miocene of Santa Cruz, Patagonia.

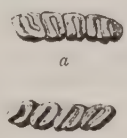


FIG. 145.

Perimys erectus Amegh. Upper Miocene of Santa Cruz. *a*, Upper, and *b*, lower tooth-row. $^1/_1$.

Subfamily 5. CHINCHILLINAE.

Usually only one enamel fold extending transversely across the grinding surface. This family probably originates in the European genus *Archaeomys*.

Prolagostomus, *Pliolagostomus* Ameghino. Santa Cruz beds. Ancestors of *Lagostomus* Brooks, fossil in the Pliocene and onwards. Also Recent.

Perimys Ameghino (Fig. 145). Colpodon beds and Santa Cruz formation of Patagonia.

Scotaeumys, *Sphodromys* Ameghino.

Megamys Laurillard. The largest fossil rodent. Pliocene and Pleistocene of Argentina.

Subfamily 6. Caviinae.

Cheek teeth composed of two, seldom more, angulated prisms.

Cephalomys Ameghino. Pyrotherium beds of Patagonia.

Eocardia, Procardia, Schistomys and *Phanomys* Ameghino. Santa Cruz. Ancestors of *Cavia.*

Cavia Pallas. *Dolichotis* Desmarest. *Kerodon* Cuv. Recent and Pleistocene of South America. Ameghino has established several new genera, *Cardiodon, Anchimys,* etc., upon Pliocene remains foreshadowing *Cavia.*

Hydrochoerus Brisson (Fig. 128, p. 102). Capybara. The largest Recent rodent. Fossil in the Pleistocene of South and North America.

Fig. 146.

Nesokerodon quercyi Schlosser. Oligocene. Phosphorites of Quercy. *a,* Mandible with P_4 (young specimen); *b,* upper D_4; *c,* lower D_4. $^3/_1$.

Subfamily 7. Issiodoromyinae.

This subfamily, restricted to the European Oligocene, may be considered on account of its dental formula and structure as transitional between the *Theridomyinae* and *Caviinae. D* with complicated structure and functioning, *P* and *M* rooted.

Nesokerodon Schlosser (Fig. 146). Teeth still displaying outer and inner enamel folds and fossettes. Phosphorites of Quercy.

Issiodoromys Croizet. Oligocene; Dept. Allier.

Suborder B. DUPLICIDENTATA (Lagomorpha).

$\frac{2}{1}$ *I, entirely covered with enamel. Second incisor—*I^3*—is small and placed directly behind* I^2. $P\ \frac{3}{2}$. $M\ \frac{3\text{-}2.}{3\text{-}2.}$ *Cheek teeth hypsodont, without roots and made up of two, less frequently of three, angular prisms. The distance between the two upper dental rows is greater than between the lower. The socket for the condyle of the lower jaw is shallow. Carpals free. Fibula articulating with calcaneum.*

This group, commonly called *Lagomorpha,* is distinguished from remaining rodents in having two upper incisors. These teeth are entirely covered with enamel, although the layers on the back and sides are considerably thinner than on the front surface. The larger of the two upper incisors has a longitudinal depression. The cheek teeth are without roots, open below, and the upper ones rather broader than long in cross-section. They are composed of prisms which appear to be compressed in an antero-posterior line and connected by cement. The inflections between the prisms of the lower teeth are all of the same depth, but the outer ones of the upper teeth are shallower than those on the inner surface. The first upper *P* and the last lower *M* have sometimes only a single prism, but the last lower *M* has, at times, three prisms. The first lower *P* and the first two upper *P* often are structurally different from the *M.* Sometimes enamel fossettes and ridges can be seen on the crown, as evidence of their bunodont and lophodont origin. Low, rooted *D* precede the *P,* and are shed as soon as the last *M* begins to function. In the milk dentition there are in the upper jaw three deciduous *I.*

Family 1. **Leporidae.** Rabbits and Hares.

$\frac{3}{2}$ *P.* $\frac{3}{3}$ *M.* P^2 *peg-like, the remaining P resembling the molars. Skull laterally compressed, clavicle incomplete. Hind legs and ears long, tail very short.*

Palaeolagus Leidy. White River Oligocene; North America.

Panolax Cope. Miocene; North America.

Lepus Linn. In North America extending from the John Day Miocene to the present day. In Europe and Asia from the Lower Pliocene to recent times.

Family 2. **Ochotonidae** (*Lagomyidae*).

$\frac{3\text{-}2}{2}$ *P.* $\frac{2\text{-}3}{2\text{-}3}$ *M. Only* P_4 *resembles M. Skull low. Clavicle complete. Hind legs and ears short. Tail lacking.*

In Europe extending from the Upper Oligocene to the modern fauna. Recent in the eastern part of Europe, in the mountain regions of Asia and North America. Fossil also in the latter continent.

Prolagus Pomel (*Myolagus* Hensel) (Fig. 147). $\frac{3.2.}{2.2.}$ From Miocene to the Pleistocene of Europe.

Titanomys v. Meyer. $\frac{3.2.}{2.2\text{-}3.}$ Upper Oligocene and Miocene. *T. visenoviensis* v. Meyer, *T. fontannesi* Depéret.

Lagopsis Schlosser. $\frac{3.2.}{2.3.}$ Miocene.

Ochotona Linck (*Lagomys* Cuv.). Recent in the northern hemisphere, fossil in the Pliocene and Pleistocene of Europe and North America.

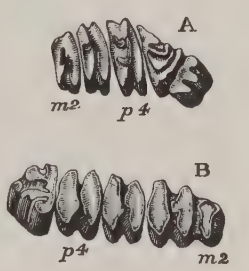


Fig. 147.

Prolagus oeningensis König. Upper Miocene of La Grive St. Alban. *A*, Upper molars. *B*, Lower molars. $^3/_1$. (After Forsyth Major.)

Geological Distribution of the Rodents.

The oldest known rodent is that from the Lower Eocene of North America (Wasatch and Bridger beds), and belongs to the genus *Paramys*, one of the *Ischyromyinae*. Accompanying this form in the Uinta beds is found *Protoptychus*, ancestor of the recent subfamily *Geomyinae*, which is now restricted to North America. The *Paramyinae* give rise in North America to the *Sciurinae* and *Haplodontinae*, the former later becoming widely distributed in Europe. The *Ischyromyinae* become extinct in the White River Oligocene, where the forms *Leporidae*, *Castorinae* and *Cricetinae* first appear. The *Castorinae* are represented in Europe at an early period, whereas the *Cricetinae* are apparently of Old World origin, and the *Leporidae* first appear in Asia and Europe in the Pliocene. Recent North American rodents are essentially the same as those of Eurasia. The *Arvicolinae* and *Ochotonidae* from the Pleistocene of Europe, and the *Erethizontinae*, originating in South America, are successors of families already found in the Tertiary.

In the Eocene of Europe, and more especially in the early Oligocene of the same region, rodents display a great diversity of forms. Besides the

Sciurinae, originating in North America, we have the *Pseudosciurinae*; the *Theridomyinae*, originally related to these; the *Hystricinae* and *Myoxinae*; and the *Cricetinae*. The last subfamily has representatives in the North American Oligocene, from which the *Hesperomyinae* are descended. The *Castorinae* appear in Europe during this period. Still earlier we find the *Ochotonidae* in Europe; their origin, however, is still obscure. All of the above-mentioned families, with the exception of *Pseudosciurinae* and *Theridomyinae*, which soon become extinct, remain in this region throughout the entire Tertiary, and some of them migrate also into Asia and Africa. The rather sparsely represented *Cricetinae* give rise to the two subfamilies *Murinae* and *Arvicolinae* in Europe. The former gradually migrate to all parts of the globe, and the latter inhabit, for the most part, the northern part of North America and Eurasia.

The *Theridomyinae* are rather important on account of their evolutionary history. They become extinct in Europe after the Lower Miocene, it is true, but attain a high degree of development slightly later in South America; they give rise not only to the *Erethizontinae* and *Capromyinae* but also to the *Octodontinae* and *Chinchillinae*. The *Issiodoromyinae*, which can be traced back to the *Theridomyinae*, in turn give rise to the *Caviinae*. The latter group appears first in the Pyrotherium beds of Patagonia. *Erethizontinae* and *Octodontinae* are found in the Colpodon beds, and are represented by many genera and species in the Upper Miocene of Santa Cruz. Thus, this rodent fauna is second in complexity only to that found in South America in the early Tertiary, in the Pleistocene and in recent times. The recent rodent fauna of South America differs from that of the Santa Cruz beds only in the presence of the *Leporidae* and *Hesperomyinae*. Contrasted with the *Hystricoidea*, which must have immigrated from Europe, these two families wandered from North America. The *Erethizontinae*, however, migrated from South to North America.

Order VII. UNGULATA.[1]

The Ungulates are distinguished by having a dentition adapted for herbivorous, seldom for omnivorous diet, and extremities adapted exclusively for terrestrial habits. The terminal phalanges are, accordingly, broad and blunt, seldom angular or irregular, and with horny hoofs.

The primitive ungulates, according to Cope, were pentadactyl and plantigrade, very like the carnivores, with short, stout extremities. The manus and pes passed through several stages of modification, as follows:

1. The plantigrade foot became transformed, by means of the infrequent use of the metapodials, into a semi-plantigrade condition. In this form the end-phalanges and the metapodials, supported and strengthened by a muscular pad, bore the full weight of the body. From this semi-plantigrade foot developed, on the one hand, the unguligrade foot; and on the other, the digitigrade. In the former the metapodials are entirely lifted from the

[1] *Cope, E. D.*, The classification of the ungulate Mammalia. Proc. Amer. Philos. Soc., 1882.—*Gregory, W. K.*, The orders of mammals. Bull. Amer. Mus. Nat. Hist., New York, 1910.—*Kowalevsky, W.*, Monographie der Gattung Anthracotherium. Palaeontographica, 1874, vol. xxii.—*Osborn, H. F.*, Evolution of mammalian molar teeth. New York, 1907.—The evolution of the ungulate foot. Trans. Amer. Philos. Soc., 1889, vol. xvi.—*Rütimeyer, L.*, Beitrage zur vergleichenden Odontographie der Huftiere. Verh. Naturf. Ges. Basel, 1863.—*Schlosser, M.*, Beiträge zur Stammesgeschichte der Huftiere. Morph. Jahrb., 1886, vol. xii.

ground and almost perpendicular, so that the end-phalanges bear the weight of the body. The digitigrade foot, a form quite rare among the ungulates (*Camelidae*), has the metapodials elevated from the ground, but all of the phalanges, protected by an elastic pad, rest on the ground.

2. The metapodials became very much elongated.

3. Certain metapodials and toes became very well developed and elongated, at the expense of the reduction or disappearance of the lateral metapodials, and frequently also of the lateral carpals and tarsals.

4. The carpals, tarsals and metapodials, which originally were arranged in part serially in parallel rows, became laterally displaced and wedged into a more or less alternating arrangement.

5. Certain carpals, tarsals and metapodials, separate in the primitive forms, became fused.

The dentition of the ungulates is of service for the classification of genera in equally important degree as the structure of their extremities. The primitive Ungulata had a complete set of teeth, all of which, with possibly the exception of the front *P*, were very closely set together. Owing to the elongation of the jaws, large diastemas were formed between the canines, incisors and anterior premolars. The incisors are always single-rooted and originally conical as in the carnivores, but through differentiation become chisel- or spade-like, developing, at times, even into tusks. Reduction in the incisors occurs, all of these teeth, particularly the upper ones, sometimes disappearing. The upper canines, which originally resembled the canines of carnivores, become either angular tusks or diminish in size, or the upper ones become entirely lost, the lower ones functioning as, and resembling, a fourth incisor (*Ruminantia*). The upper molars seldom remain tritubercular, and have two secondary cusps (conules) even in this earliest stage. A second large inner cusp (hypocone) is developed from either the metaconule or the cingulum. If the cusps connect so as to form ridges or crescents, they pass from the original condition of bunodont into lophodont or selenodont teeth. Further differentiation occurs through the greater development of the base of the tooth either through the formation of a cingulum, or of enamel folds, or of cement accumulation. As a rule, the lower molars can easily be referred to the primitive tritubercular-sectorial type, with a high tricuspate trigonid and a low, likewise tricuspate talonid. Through loss of the paraconid and the further development, both in height and breadth, of the talonid, quadricuspate teeth result, which may be distinguished from the upper molars principally by reason of being less broad. These, too, may become lophodont or selenodont. The last lower molar has frequently an unpaired large rear cusp or a semicircular ridge. The premolars remain more primitive than the molars in all ungulates. A homoeodont dentition is attained only in very highly specialised forms. The reduction of the cheek teeth begins with the first *P*, and includes, at the most, but two or three *P*.

Originally the cheek teeth of the ungulates were low and brachyodont, the lower ones with two roots and the upper with three. Through the dichotomy of the two roots of the lower molars, and the broad middle root of the upper, teeth with four roots each result. Frequently the crown becomes very high in herbivorous animals, finally converting the teeth into hypsodont or prismatic columnar teeth, which are pushed up in the gums as their surface is worn down through use, and develop roots only later in life.

The milk dentition consists usually of incisors, canines and cheek teeth. The *ID* and *CD* are unlike the *I* and *C* only in that they are weaker. The *PD*, on the contrary, offer many characteristic and systematically important differences. Their number may diminish from four to three, but may also remain unchanged, even though they are followed by only three *P*. The posterior *D* has always the construction of a molar. In the lower jaw of the artiodactyls D_4 has a third, although small, pair of cusps, and the lower D_3 of the perissodactyls is often more complicated than the molars.

The skull of the ungulates exhibits considerable differentiation. The cranial cavity of the most primitive ungulates is very small, the hemispheres of the cerebrum are slightly furrowed and leave the cerebellum uncovered. The size and complexity of the cerebrum of the higher types increase considerably. The skull of the earliest representatives of the ungulates has no particularly distinguishing features. It is low, has a flat roof and a well-developed sagittal crest on the narrow cranium. Specialisation in several directions takes place, however, with the gradual evolution of the group. Thus the frontals may be filled with air-cavities, or may bear horns, as in artiodactyls. The basifacial axis, parallel as a rule to the basicranial axis, may in some cases become inclined to it. With enlargement and development of the nasals and the orbits the skull assumes a very characteristic appearance, which may become still more intensified by the ossification of certain protuberances on the snout.

The *Ungulata* are now distributed in all parts of the globe with the exception of Australia. In the Tertiary they were scarcely less abundant than now.

Only those forms which had bunodont ancestors, or at least whose ancestors possessed a normal canine and display well-marked specialisations in the extremities, can be properly included among the *Ungulata*. Thus they can be divided into five suborders: *Condylarthra*, *Litopterna*, *Perissodactyla*, *Artiodactyla* and *Amblypoda*. The relationship of the last suborder to the bunodont forms is, however, somewhat uncertain.

Suborder A. CONDYLARTHRA Cope.[1]

Extinct plantigrade ungulates with pentadactyl extremities. Astragalus with elongated neck, usually with foramen, and convex distal articular surface. Carpals arranged in two rectilinear series. Dentition complete. Cheek teeth bunodont. Humerus with entepicondylar foramen. Femur with third trochanter.

The *Condylarthra* are, with the exception of a few scattered remains from the oldest European Eocene, restricted to the oldest Tertiary of western North America (Puerco, Torrejon and Wasatch beds). They are unquestionably the most primitive of ungulates, from which the perissodactyls, artiodactyls, and possibly the South American *Litopterna* originated. They display many creodont features in their cranial and skeletal structure, and probably arose from a common stock.

[1] *Cope, E. D.*, The Condylarthra. Amer. Naturalist, 1884, p. 790, 892. Trans. Amer. Philos. Soc., 1888, p. 298.—*Matthew, W. D.* Bull. Amer. Mus. Nat. Hist., New York, 1897, p. 293.—*Matthew* and *Granger*. *Ibid.*, 1915.—*Osborn, H. F.*, and *Earle, C.* *Ibid.*, 1895, p. 47.—*Osborn, H. F.* *Ibid.*, 1898, p. 159.

The low, elongate skull is but slightly specialised and combines characters of the creodonts and primitive perissodactyls and artiodactyls. The orbits are wide open posteriorly, the profile outline of the skull is almost horizontal, the cranium has a sagittal crest, the brain is very small and the cerebellum lies behind the smooth hemispheres of the cerebrum. The postglenoid process is very well developed, and the dentition is complete. The incisors and canines are like those of the creodonts and the primitive perissodactyls and artiodactyls. The *P* are much simpler than the brachyodont, three or four rooted tritubercular or quadritubercular molars.

The dental formula is complete; the last milk cheek teeth are similar to the first molar. The upper *M* have two outer, usually one inner, and two middle cusps. The lower *M* have four primary cusps and one or two secondary cusps.

The plantigrade or semidigitigrade extremities (Fig. 148) have five toes in the manus and pes, of which the three inner digits are more strongly developed than the two outer ones. The clavicle is usually present. The humerus has always an entepicondylar foramen, and the femur a third trochanter. Radius and ulna, as well as tibia and fibula, remain distinct. The fibula ends, as in carnivores, without calcaneal articulation. The two rows of carpals are almost serially arranged in *Phenacodus*, the centrale absent; in other *Condylarthra* the carpals are alternating and an os centrale is present. The tarsus is essentially the same as in the creodonts. The concave articular surface of the astragalus extends rather far down on the navicular and touches the cuboid only on the lateral surface. The trochlea often has a perforation, the "astragalar foramen." The terminal phalanges are distally flattened, but are pointed and quite often bifid, as in the case of the creodonts.

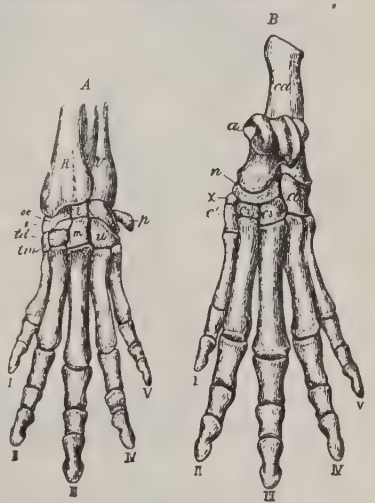


FIG. 148.

Hyracops socialis Marsh. Lower Eocene Wasatch, Wyoming. *A*, Left fore-foot. *B*, Left hind-foot. 2/3. (After Marsh.) R, Radius; U, ulna; *a*, astragalus; *ca*, calcaneum; *cb*, cuboid; *ce*, centrale; c^{123}, cuneiforms; *l*, lunar; *m*, magnum; *n*, navicular; *p*, pisiform; *s*, scaphoid; *td*, trapezoid; *tm*, trapezium; *u*, unciform; *x*, epicuneiform.

In external appearance, the *Condylarthra* doubtless resembled the omnivorous carnivores rather than the ungulates. The character of the articulations in the manus and pes did not permit very swift movement, while the dentition suggests subsistence on both vegetable and animal food. The largest forms attained the dimensions of the wolf; the smallest those of the rabbit.

Family 1. **Mioclaenidae** Osborn and Earle.

Upper molars subtriangular, broader than long, without a second internal cusp; lower molars usually quinquetubercular, the anterior cusp (paraconid), however, if present, very small. Premolars simple, the second and third only with internal

cusps. Skeleton little known. Basal Eocene; Puerco and Torrejon beds, New Mexico.

The largest species attained the size of the fox. The crescentic form of the external cusps of the lower molars is very distinctive. It is probable that these forms mark the rise of the artiodactyls.

Fig. 149.

Mioclaenus lemuroides Matthew. Lower Eocene of Torrejon beds, New Mexico. *A*, Mandible, and *B*, upper tooth-row, $P^3 - M^3$. 1/1. (After Matthew.)

Mioclaenus Cope (Fig. 149). Dental series continuous. Premolars relatively short. *M. turgidus, acolytus* Cope. *M. lemuroides* Matthew.

Protoselene Matthew. Premolars compressed (*P. opisthaca* Cope).

Oxyacodon Osborn and Earle (*Anisonchus agapetillus* Cope). Very simple short premolars. Lower molars quinquetubercular. Lowermost Eocene; Puerco beds, New Mexico.

Family 2. **Periptychidae** Cope.

Upper molars tritubercular. Upper and lower premolars rather large, usually single cusped, sometimes with a low internal tubercle. Tibial articular surface of the short broad astragalus rounded, medially concave. Navicular laterally in contact with calcaneum and cuboid. Lowermost Eocene; Puerco and Torrejon beds, New Mexico.

According to Matthew, these forms, at least in the structure of their extremities, are allied to the *Pantolambdidae* and belong, therefore, to the *Amblypoda*, but they differ widely in having bunodont molars.

Periptychus Cope (Fig. 150). Teeth highly specialised, enamel very strongly developed. Upper molars almost quadrate. Premolars very large, grooved vertically. This form nearly equalled the sheep in size. Torrejon beds; New Mexico.

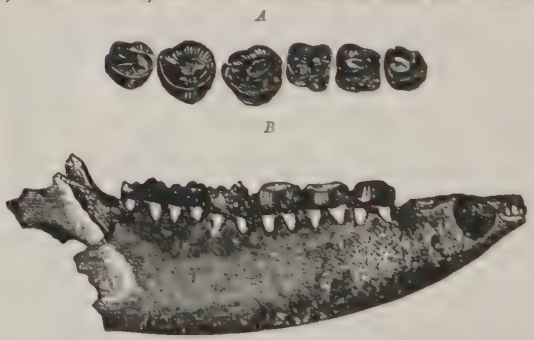


Fig. 150.

Periptychus rhabdodon Cope. Lower Eocene of Torrejon beds, New Mexico. *A*, Upper cheek teeth. *B*, Right ramus of lower jaw. 1/3. (After Cope.)

Ectoconus Cope. Of equally large size as the preceding form; and with multituberculate molars. Puerco beds; New Mexico.

Haploconus, Hemithlaeus, Anisonchus (*Zetodon*) Cope, and *Conacodon* Matthew, are all of smaller size. Upper molars much broader than long, without a second internal cone, but with anterior and posterior cingula. Lower third molars with a short talonid. Puerco and Torrejon beds; New Mexico

Family 3. Phenacodontidae Cope.

Upper molars quadrangular, somewhat broader than long, with two external, two intermediate, and two internal cusps. First and second premolars simple in both jaws; third premolar with from one to two accessory tubercles; fourth inferior premolar submolariform, but narrow; fourth superior premolar large, with two external and one internal cusps, and two small intermediate tubercles. Lower molars with three cones on the anterior half of the crown and on the talonid. Tibial facet of the astragalus medially grooved; fibula articulating with the astragalus only; navicular coming in contact laterally with cuboid and calcaneum. Fore and hind feet pentadactyl, semidigitigrade?

FIG. 151.

Phenacodus primaevus Cope. Lower Eocene of Wasatch beds, Wyoming.
A, Skeleton greatly reduced in size. *B*, Upper and lower teeth of one side. $^2/_3$. (After Cope.)

The *Phenacodontidae* are distinguished from the *Periptychidae* by the complication of the premolars, the higher and more compact tarsus, and the longer neck of the astragalus. Of the two species of the genus *Phenacodus* represented by skeletons, from the Eocene Wasatch beds of Wyoming, *P. primaevus* Cope (Fig. 151) attained the size of the wolf, while *P. wortmani* Cope, from the Wind River beds, was as large as the fox. The dorsal vertebrae are fifteen in number, with from five to six lumbar vertebrae.

Tetraclaenodon Scott (*Protogonia* Cope; *Euprotogonia* Earle) (Fig. 152). Teeth bunodont, very similar to those of *Hyracotherium*. Extremities slender. Lower Eocene; Torrejon beds, New Mexico and Montana.

Protogonodon Scott (*Mioclaenus pentacus* Cope). This very large form, with quinquetubercular molars, is perhaps ancestral to certain artiodactyls, such as *Achaenodon* and *Entelodon*. Lower Eocene; Puerco beds, New Mexico.

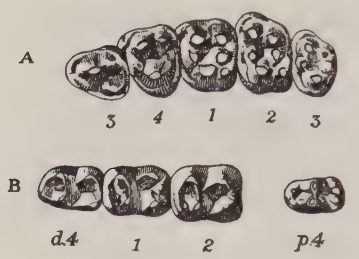
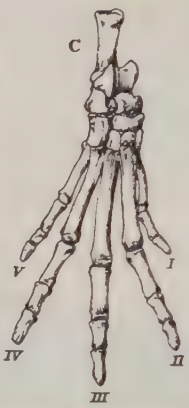


FIG. 152.

Tetraclaenodon puercensis Cope sp. Lower Eocene of Torrejon beds, New Mexico. *A*, Upper molars. *B*, Lower molars (D_4, M_{1-2}, P_4). 1/1. (After Osborn.) *C*, Hind foot. 1/2. (After Matthew.)



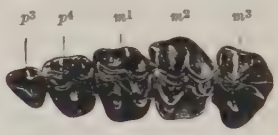


FIG. 153.

Meniscotherium terrae-rubrae Cope. Wasatch Strata of Lower Eocene, New Mexico. The three upper molars and last two premolars. 1/1. (After Cope.)

Family 4. Meniscotheriidae Cope.

Tooth series nearly continuous. Superior molars quadritubercular, with W*-shaped ectoloph, two crest-like curved intermediate tubercles, and two unequal conical internal cusps. Posterior premolars tritubercular. Inferior molars and last premolar composed of two* V*-shaped crescents, the three anterior premolars simple. Astragalus strongly elongate, the distal articular surface rounded.*

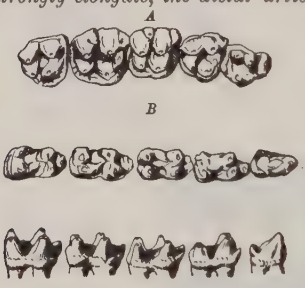


FIG. 154.

Pleuraspidotherium aumonieri Lemoine. Lower Eocene, Cernays, near Rheims. *A*, Upper molars. *B*, Lower molars. 7/8. (After Lemoine.)

Meniscotherium Cope (*Hyracops* Marsh) (Figs. 148, 153). Lower Eocene (Wasatch beds); New Mexico.

Family 5. Pleuraspidotheriidae Lemoine.

Dentition complete. Incisors, canines and first premolars conical. A small diastema between the first and second or third premolars. Superior molars, with four V*-shaped cones and a weakly developed protoconule. Fourth premolar like the first molar; third premolar with simple internal conical tubercle. Inferior molars, as well as third and fourth premolars, with four conical tubercles in pairs and one odd anterior cusp. Feet pentadactyl; terminal phalanges slender with slight lateral wing-like expansions distally. Astragalus with broad trochlea and short neck.*

Pleuraspidotherium Lemoine (Fig. 154). This form, from the Lowermost Eocene of Cernays, near Rheims, may possibly have phylogenetic relations with European perissodactyls.

Suborder B. LITOPTERNA Ameghino.[1]

Extinct, digitigrade ungulates with serially arranged carpals and tarsals, manus and pes with five (?), three or one digits. Astragalus with deep trochlea and convex

[1] *Ameghino, Flor.*, Contribución al conocimiento de los mamíferos fósiles de la Republica Argentina. Actas Acad. Nac. Cordoba, 1889, vol. vi.—Sur les ongulés fossiles de l'Argentine.

distal articular surface. Calcaneum articulating with fibula. Dentition complete or with incisors reduced. Teeth often in close series. Cheek teeth bunolophodont, selenolophodont, usually brachyodont. Humerus without entepicondylar foramen. Terminal phalanges broad.

The Litopternine suborder of ungulates is restricted to South America. It developed from a North American bunodont condylarth ancestor, and in so doing acquired a perissodactyl-like dentition and reduction of the outer digits of the feet such as occurs in many perissodactyls.

The reduction sometimes involves only the first and fifth digits, but the second and fourth may also be reduced, either becoming shorter and thinner, or becoming mere rudiments. The teeth become only exceptionally hypsodont, and those which remain brachyodont become more highly specialised in that the roots are further divided, so that each tooth in the lower jaw is provided with four roots. They have, in common with the *Notoungulata*, a short metaloph on the upper molars, but are distinguished from these, not only because they are brachyodont, but also because the trigonid and the talonid of the lower molars are about the same size. The upper molars have two outer cusps, which form an ectoloph made up of para- and metastyle, a large protocone, two secondary cusps and a small hypocone. The protocone is joined with the protoconule to form an oblique protoloph, the short metaloph is made up of the hypocone and the rather prominent back surface of the tooth. The metaconule is connected rather with the protocone than with the hypocone. The lower molars consist of two semicrescental ridges, of uniform size. The inner cusp arising to one side of the second ridge, a feature which is very characteristic of the *Notoungulata*, is found only in the *Macraucheniidae*. The last of the incisors may become vestigial, and the second larger than the first. All of the teeth are, as a rule, brachyodont and are set rather closely. The bones of the skeleton are very similar to those of the perissodactyls.

Family 1. **Bunolitopternidae.** (*Didolodidae* Scott.)

Upper molars with two outer cusps, which are more or less separated from the rest, two large inner cusps, of unequal size, and frequently with a number of secondary cusps. Lower molars with two conical inner cusps and two V*-shaped outer cusps. Premolars much simpler than the molars.*

This family is distinguished from the condylarths principally by the small canines and the lack of a diastema. The extremities were possibly pentadactyl.

Among the numerous genera which Ameghino established, basing his classification on isolated molars, *Lambdaconus*, *Oroacrodon*, etc., seem to lead to the *Macraucheniidae*; *Notoprogonia*, *Lonchoconus*, *Proectocion*, etc., to the *Proterotheriidae*; and others, such as *Ricardolydekkeria*, *Josepholeidya*, *Argyro-*

Rev. Jard. Zoolog. Buenos Aires, 1894.—Énumération synoptique des mammifères fossiles éocènes de Patagonie. Buenos Aires, 1894.—Mammifères crétacés de l'Argentine. Bol. Instit. Geograf. Argent. Buenos Aires, 1897, vol. xviii.—Recherches de morphologie sur les molaires supérieures des ongulés. Anal. Mus. Nac. Buenos Aires, vol. ix., 1904.—*Burmeister, Herm.* Anal. Mus. Publ. Buenos Aires, 1864, vol. i.—Nova Acta Acad. Leop. Carol., 1885, vol. xlvii.—*Cope, E. D.*, The Litopterna. Amer. Naturalist, 1889, vol. xxv.—*Gaudry, A.*, Fossiles de Patagonie. Mém. Soc. Géol. France. Paléont. vol. xiii. 1904.—Annal. de Paléont., 1906.—*Lydekker, R.*, Palaeontologia Argentina. Anal. Mus. de La Plata, 1893.—*Scott, W. B.*, Litopterna of the Santa Cruz Beds. Rep. Princeton Exped. Patagonia. Princeton, 1910.

lambda, etc., had no descendants. The dentition only of *Didolodus* (Fig. 155) is comparatively well known.

All members of this family are limited to the Eocene (Notostylops beds) and the Oligocene (Astraponotus beds) of Patagonia.

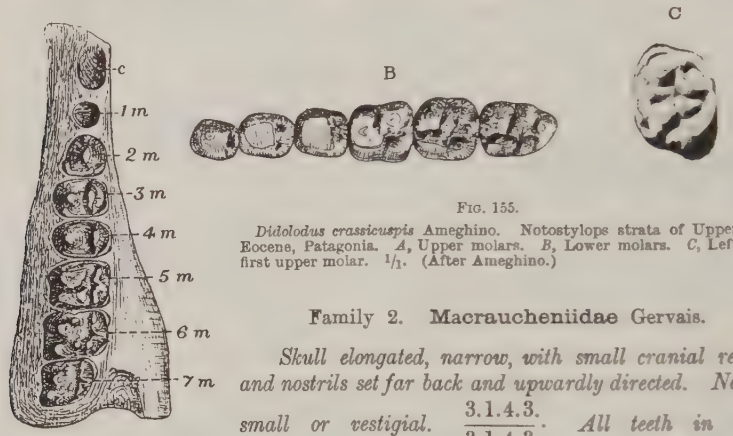


Fig. 155.

Didolodus crassicuspis Ameghino. Notostylops strata of Upper Eocene, Patagonia. *A*, Upper molars. *B*, Lower molars. *C*, Left first upper molar. $^1/_1$. (After Ameghino.)

Family 2. **Macraucheniidae** Gervais.

Skull elongated, narrow, with small cranial region and nostrils set far back and upwardly directed. Nasals small or vestigial. $\frac{3.1.4.3.}{3.1.4.3.}$ *All teeth in close series, and progressively changing from the simple anterior type to the complex molars. Molars selenolophodont. Lower molars consisting of two semicrescental ridges and one inner cusp. Upper molars with* W*-shaped ectoloph, a large protocone, which is united with the protoloph and metaloph, and a small hypocone. Manus and pes tridactyl. Femur with third trochanter. A keel is well developed only on the hinder side of the metapodials.*

The *Macraucheniidae* originate in the Eocene of Patagonia with bunodont-brachyodont forms and become extinct in the Pleistocene of Argentina with selenolophodont-hypsodont forms. They attain to a considerable size and are distinguished by very high, digitigrade extremities, long neck and elongated skull, with nostrils situated far back. The teeth are very like those of *Anoplotherium*. Anterior and posterior edge of the inner side of the upper molars and premolars form a high ridge. The mode of life seems to have been aquatic.

Coniopternium, *Protheosodon* Ameghino

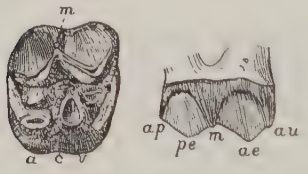


Fig. 156.

Protheosodon conifernus Ameghino. Pyrotherium strata of Lower Miocene. Upper molar. $^1/_1$. (After Ameghino.)

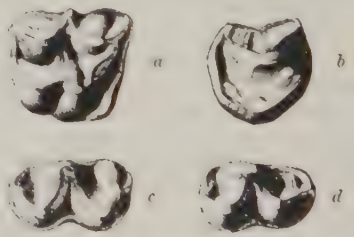


Fig. 157.

Cramauchenia patagonica Ameghino. Middle Miocene. Colpodon beds of Patagonia. *a*, Upper M^2; *b*, upper P^3; *c*, lower M_2; *d*, lower M_3. $^1/_1$.

(Fig. 156). Lower Miocene (Pyrotherium beds). *Cramauchenia* Ameghino (Fig. 157) and *Theosodon* Ameghino. Miocene of Santa Cruz. All brachyo-

dont. Orbits open posteriorly, nasals short and extending far forward. Manus and pes tridactyl.

Oxyodontherium, *Scalabinitherium* Ameghino. Pliocene; Argentina. Nasal opening above molars. Teeth rather hypsodont.

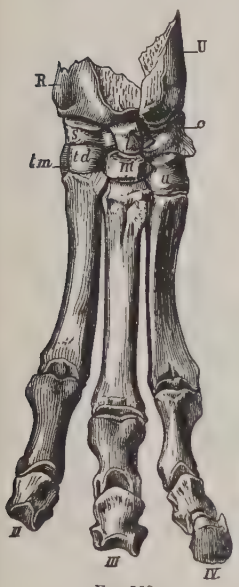


Fig. 158.

Macrauchenia patachonica Owen. Manus. 1/6. (After Gervais.)

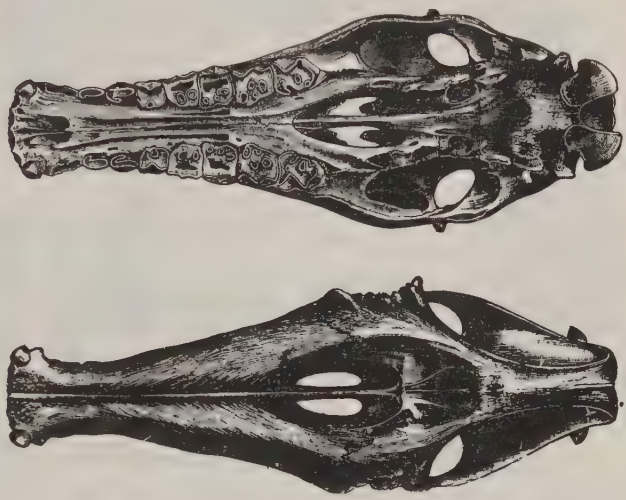


Fig. 159.

Macrauchenia patachonica Owen. Pampas formation of Pleistocene, Buenos Aires, Argentina. Inferior and superior aspect of skull. 1/6. (After Bravard.)

Macrauchenia Owen (*Opisthorhinus* Brav.) (Figs. 158-160). Nasals rudimentary, a large nasal opening on the centre of the skull. Orbits posteriorly closed. Pleistocene, Argentina.

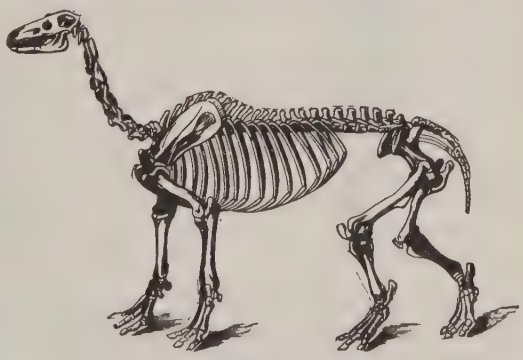


Fig. 160.

Macrauchenia patachonica Owen. Restored skeleton. Much reduced. (After Burmeister.)

Family 3.

Proterotheriidae

Ameghino.

Skull rather long with tapering muzzle. Nasals long. Orbits posteriorly closed. $\frac{1.0.4.3.}{2.1.4.3.}$ *All teeth brachyodont. In the upper jaw a small diastema. Upper molars with* W*-shaped ectoloph, two large inner cusps, of unequal size, and one or two secondary cusps. The last premolars frequently molariform. Lower molars and P* 2-4 *with two semicircular ridges and four roots. I enlarged, canine small. Extremities with three or one toe, only*

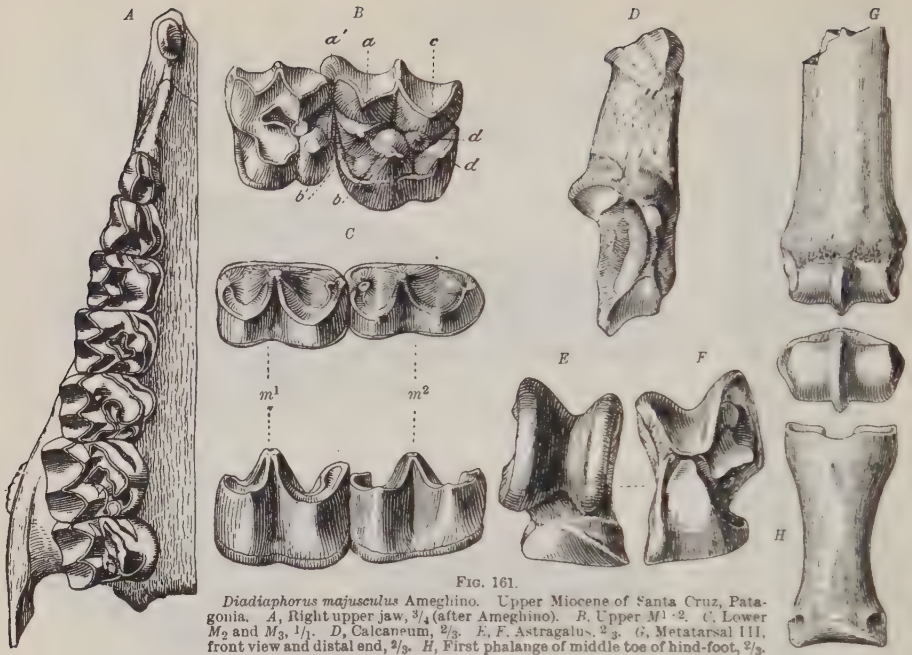


FIG. 161.

Diadiaphorus majusculus Ameghino. Upper Miocene of Santa Cruz, Patagonia. *A*, Right upper jaw, 3/4 (after Ameghino). *B*, Upper M^1-2. *C*, Lower M_2 and M_3, 1/1. *D*, Calcaneum, 2/3. *E*, *F*, Astragalus, 2/3. *G*, Metatarsal III, front view and distal end, 2/3. *H*, First phalange of middle toe of hind-foot, 2/3.

FIG. 162.

Epitherium laternarium Ameghino. Pleistocene, Monte Hermoso, Argentina. Right hind-foot. 1/3. (After Ameghino.)

FIG. 163.

Thoatherium minusculum Ameghino. Upper Miocene of Santa Cruz, Patagonia. Lower jaw. 2/3. (After Ameghino.)

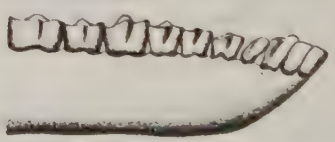


FIG. 164.

Adiantus patagonicus Ameghino. Colpodon beds. Middle Miocene of Patagonia. Lower jaw without M_3. 4/5.

the third digit is strongly developed; keels extending over the entire distal surface of the metapodials.

Epitherium Ameghino (Fig. 162). Second and fourth toe short and thin. Earliest Pleistocene. Monte Hermoso, Argentina. *Eoauchenia* Ameghino. Same locality. Crowns of the teeth high.

Diadiaphorus (Fig. 161) and *Proterotherium* Ameghino. Miocene and Pliocene. Tridactyl. Isolated pillars on the inner side of the semicircular ridge of the lower molars. Ulna reduced.

Brachytherium Ameghino. Pliocene of Argentina.

Licaphrium Ameghino, *Tetramerorhinus* Ameghino. Miocene of Patagonia. *Thoatherium* Ameghino (Fig. 163). Same locality. With only one toe.

Eoproterotherium, *Deuterotherium* Ameghino. Lower Miocene. Pyrotherium beds of Patagonia.

Family 4. **Adiantidae** Ameghino.

Adiantus Amegh. (Fig. 164). *Proadiantus* Ameghino. Miocene of Patagonia. Only lower jaw is known, which has very close tooth rows, 3.1.4.3.; incisors and canines are chisel-shaped, molars rather high and composed of two crescents and inner cusps. Systematic position uncertain.

Suborder C. **PERISSODACTYLA** Owen. (**Mesaxonia** Marsh.)

Odd-toed Ungulates.[1]

Digitigrade hoofed quadrupeds with the middle digit much more developed than the others; usually with three digits in the pes, from three to four in the manus, sometimes with only one toe in each foot. Astragalus with deeply grooved pulley-like articulation, flattened distally. Carpal and tarsal bones alternating. Dentition usually complete. Cheek teeth lophodont, more rarely bunodont. Femur with third trochanter. Fibula not articulating with calcaneum.

The perissodactyls constitute a division of herbivorous ungulates extremely abundant in forms, only three genera (*sensu lato*) of which still exist—*Tapirus*, *Rhinoceros* and *Equus*. In former geological periods, however, that is, from the earliest Eocene to the Pleistocene, they had a wide distribution and were represented by numerous genera and species. They are usually characterised by the great development of the third or middle digit in the fore- and hind-feet, which in the most specialised forms (*Equus*) alone bears the weight of the body, and in almost all cases the main axis of the extremities passes through it.

The skull acquired an elongated form through the excess in weight of the facial bones over the brain case. The occiput slopes abruptly, the condyles are convex transversely, and the large temporal fossae are surmounted by a temporal crest. The nasal bones stand out freely above the narial apertures, which open laterally, extend far backward, and are bounded below

[1] *Cope, E. D.*, The Perissodactyla. Amer. Nat., vol. xxi., p. 985, 1887.—*Osborn, H. F.*, Mammalia of the Uinta Formation. III. The Perissodactyla. Trans. Amer. Phil. Soc., vol. xvi., part iv., 1889.—The Evolution of the Ungulate Foot. *Ibid.*—*Osborn, H. F.*, and *Wortman, J. L.*, Perissodactyls of the Lower Miocene White River Beds. Bull. Amer. Mus. Nat. Hist., pp. 343-375, 1895.—*Owen, Richard.* Quart. Journ. Geol. Soc. London, vol. iv., p. 103, 1847.—*Stehlin, H. G.*, Die Säugetiere der Schweiz. Eocän. Abh. Schweiz. Paläont. Gesellsch., 1903, 1904, 1906.

by the premaxillaries and frequently by the maxillaries also. In some forms (*Rhinoceridae*), the nasal bones bear horns on rough cushion-like surfaces, or these elements may be furnished with bony protuberances of various sizes (*Titanotheriidae*). As a rule, the orbits are wide open posteriorly, and only in the youngest equine genera are completely surrounded by bone. The zygomatic process of the squamosal bone enters considerably into the formation of the zygomatic arch.

In its typical development, the permanent dentition of the perissodactyls consists of three incisors, one canine, and seven cheek teeth in each jaw above and below. This dental formula holds good for all Eocene genera. In younger and more progressive forms, the modernising of the dentition brings about a reduction, sometimes even a complete suppression, of incisors, of upper (more rarely also of lower) canines, and of the most anterior premolars. In more primitive forms, the cheek teeth are brachyodont; in some more specialised genera, prismatic. The older perissodactyls generally have heterodont, the younger, homoeodont cheek teeth. The original quadritubercular (more correctly sextubercular) crown very seldom remains absolutely bunodont, the cusps being usually united by ridges (lophodont). Through the intercalation of smaller outgrowths on the outer side of the ectoloph (parastyle, mesostyle and metastyle) and on its inner side (*crista*) and on the inner side of the transverse crests (*crochet* and *antecrochet*) of the upper cheek teeth, the crown of the tooth becomes greatly strengthened; in more specialised forms, a covering of cement also not infrequently occurs above the enamel.

The milk dentition consists of incisors, canines and cheek teeth; of these the first two correspond with those of the permanent dentition. The milk cheek teeth, on the contrary, resemble their successors only in homoeodont forms; in heterodont forms, the two posterior milk teeth are like the anterior molars, and as a rule only the most anterior is characterised by simpler shape.

The vertebral column is composed of seven cervical vertebrae, twenty to twenty-six dorso-lumbars, from five to six sacrals, and at least thirteen or more caudals. A clavicle is wanting. The humerus is short, stout, without entepicondylar foramen, and the olecranon fossa is never perforated. The radius and ulna are sometimes equally developed and separate, sometimes anchylosed distally.

In the carpus, the proximal series consists of four ossicles (scaphoid, lunar, cuneiform and pisiform), the distal row comprising the trapezium, trapezoid, magnum and unciform. The centrale is absent. Fusion of the adjacent ossicles never occurs, but through a lateral shifting of the distal series and an increase in the vertical diameter, an exceedingly firm interlocking of the carpal elements is brought about. The scaphoid is no longer exclusively supported by the trapezoid, as in *Phenacodus*, but by the trapezoid and magnum, and frequently the facet of the magnum is considerably larger than that of the trapezoid. The lunar rests on the magnum and unciform, and only the cuneiform has a single distal ossicle (the unciform) underlying it. In the forms with three digits subequal in length, the carpus is slender and proportionally high; in the later equines with unusually stout middle digits, the magnum gains considerably in extent, pushes the unciform as well as the trapezoid to the side, and forces the trapezium quite out of the carpus, so

that finally it entirely disappears. Of the metacarpals, the maximum number is four, three are usually present, while in the horse only one, the third metacarpal, is functional. The pollex is always absent; the fifth digit, when present, remains shorter than the other digits. The metacarpals with their slightly concave proximal articulations force themselves in somewhat between the carpals, and thus exhibit an alternating arrangement. The metapodials vary greatly in length. In general the lengthening of the metacarpals signifies advance and usually goes hand in hand with the reduction of the lateral digits. As the weight of the body is gradually transferred to the single middle digit, there is thus formed on the distal convex articulation of the third metacarpal a distinct median ridge, which prevents a lateral displacement of the digit. In the older three-toed or four-toed perissodactyls, these keels are developed only on the posterior side of the articulation. The triangular, distally flattened terminal phalanges are encased in hoofs.

The femur is characterised by a prominent, often remarkably well-developed third trochanter. In the forms in which the median digit is less dominant, the tibia and fibula are complete and separate for their entire length; in the later *Equidae*, the fibula is reduced to a short proximal splint bone, and its distal end anchylosed to the tibia.

Of the tarsal bones, the calcaneum (Fig. 165) has an elongated truncated tuberosity (*tuber calcis*) with a rugose terminal surface, and a sustentaculum directed inward, which supports the astragalus, and is furnished with three facets. The astragalus (Fig. 166) has above and in front a deeply grooved pulley-like articulation (*t*) for the tibia, on the inner and posterior sides three facets for the calcaneum, and on the truncated, either plane or slightly convex distal surface a large facet for the navicular (*n*) and usually a small one for the cuboid (*cub*). Between the bones of the proximal and distal series lies a low navicular, which is completely covered by the astragalus and in turn is supported by the three cuneiforms of the distal series. The cuboid is high, carries the calcaneum, but likewise always articulates with the astragalus, except in *Moropus* in which the cuboid does not touch the astragalus; a typical character of *Meniscotherium* of the early Tertiary. Fusion of the two inner cuneiforms occurs only in the more specialised *Equidae*; otherwise all the tarsals remain distinct. The reduction of the lateral digits is more complete and constant in the hind-foot than in the fore-foot (Figs. 167, 173). The hind-foot is therefore either tridactyl or in the later *Equidae* monodactyl. The metatarsals with their usually plane proximal articular surfaces do not push in between the tarsals.

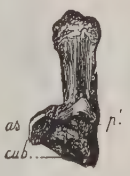


FIG. 165.

Palaeotherium. Calcaneum. *as*, *p'*, Facet for the astragalus; *cub*, facet for the cuboid.

FIG. 166.

Palaeotherium. Astragalus. *t*, Trochlea; *n*, *cub*, facet for the navicular and cuboid; *c*, *c'*, surface adjacent to the calcaneum; *a*, hollow for the lower end of the tibia.

The perissodactyls are divided into five families as follows: *Tapiridae*, *Rhinoceridae*, *Equidae*, *Titanotheriidae* and *Chalicotheriidae*. Of these the first four may be traced back to a common ancestral form, which probably was very like the condylarth genus *Tetraclaenodon*.

Family 1. **Tapiridae** Gray.[1]

Nasal bones, projecting freely. Dentition: $\frac{3.\ 1.4\text{-}3.3.}{3\text{-}2.1.4\text{-}3.3.}$. *Incisors chisel-shaped; canines conical; cheek teeth brachyodont. Premolars primitively simpler than molars, afterwards resembling them. Upper molars with two external cusps united with each other, and two straight transverse ridges uniting the two external cusps with the two internal ones. Parastyle strong. Inferior molars with two transverse crests directed either at right angles or obliquely to the longitudinal axis of the crown. Manus generally with four digits; pes tridactyl.*

The tapirs include large, medium-sized and small, hoofed quadrupeds, a single genus of which still exists in tropical America and in southern Asia. The fossil forms first appear in the Lower Eocene of Europe and North America, continue into the Pliocene on both continents, and in the Pleistocene have withdrawn to eastern Asia and America. Their nearest affinities are with the *Rhinoceridae*.

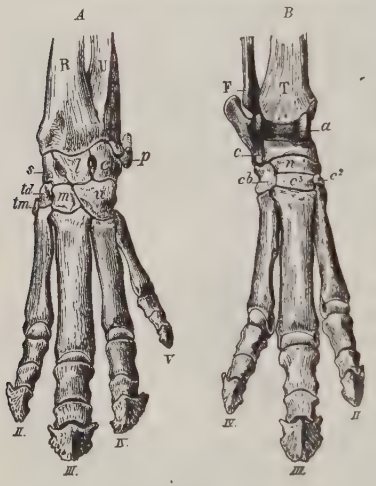


Fig. 167.

Tapirus americanus Linn. Recent. *A*, Left fore-foot. *B*, Right hind-foot. 1/5.

With the exception of *Colodon*, *Lophiodon* and *Tapirus*, all tapirs have a complete dentition. As a rule, the canines are separated from the cheek teeth by a diastema; the latter teeth are always low (brachyodont) and the crown is surrounded by a basal cingulum, which on the antero-external edge of the teeth in the upper jaw forms a more or less well-developed third pillar (parastyle). The transverse ridges uniting the internal and external tubercles of the cheek teeth are nearly rectilinear (ortholophodont). In the lower jaw, the anterior side of the original V-shaped crest is entirely obliterated; hence, as a rule only the posterior side forms the simple transverse crest. In all genera of the early Tertiary, the premolars are characterised by their simpler form, the upper jaw frequently by the tritubercular structure of the molars. In existing tapirs, the reduction is confined to the most anterior premolar, the other premolars having acquired the appearance of true molars. In the upper jaw, four premolars are usually present; in the lower jaw, the number is four or three, the milk teeth preceding them being essentially like the molars. In many genera, a suppression of the most anterior premolar in the lower jaw occurs, while

[1] *Depéret, Ch.*, Études sur les Lophiodons. Arch. Mus. Lyon, 1903. — *Filhol, H.*, Études sur les vertébrés fossiles d'Issel. Mém. Soc. Géol. France, 1888. — *Gaudry, A.*, La dentition des ancêtres des Tapirs. Bull. Soc. Géol. France, p. 315, 1897. — *Hatcher, J. B.*, Recent and Fossil Tapirs. Amer. Journ. Sci., vol. i., pp. 161-189, 1896. — *Maack, G.*, Unters. über Lophiodon von Heidenheim. Jahresber. naturhist. Ver. Augsburg. 1865. — *Meyer, H. von*, Fossile Reste des Genus Tapir. Palaeontogr., vol. xv., 1867. — *Osborn, H. F.*, and *Wortman, J. L.*, Bull. Amer. Mus. Nat. Hist., New York, 1892. — *Wortman, J. L.*, and *Earle, C.*, *ibid.*, 1893.

the upper jaw usually retains the full number (four). Only the Eocene genus *Lophiodon* is remarkable as exhibiting but three premolars above and below. The skull of the tapir is elongated, the snout slender, the brain cavity moderately large. Posteriorly the orbits are not surrounded by bone, the nasal bones stand out freely and in the older forms are very long and massive, but in *Tapirus* are short and triangular, leaving space for a short proboscis. The narial opening is large and much prolonged backward; the postglenoid and paroccipital processes are well developed. The extremities (Fig. 167) have moderate length, are more slender than those of most rhinoceroses, yet are more robust than those of most horses. The radius and ulna remain entirely separate, and are about equally developed. In the carpus, the scaphoid rests on the trapezoid and magnum, the lunar on the magnum and unciform. The magnum bears the principal weight, and is supported by the second and third metacarpals. In all well-known genera, the fore-foot is tetradactyl; the hind-foot, tridactyl. In the latter, the femur bears a moderately well-developed third trochanter, while the fibula is always complete. The astragalus has a grooved trochlea, distally a large flat articular surface for the navicular and a small one for the cuboid. The structure of the carpus and tarsus exhibits no essential change during Tertiary time.

Subfamily 1. Lophiodontinæ Gill.[1]

Upper and lower molars with two oblique transverse crests. All, or only the two anterior premolars, simpler than the molars.

Fossil in the Eocene of Europe and North America only.

Heptodon Cope. Dental formula: $\frac{3.1.4.3.}{3.1.4-3.3.}$. All premolars simpler than the molars. Third lower *M* with small third lobe. Lower Eocene (Wasatch and Wind River beds); Wyoming. *H. ventorum*, *H. calciculus* Cope.

Helaletes Marsh (*Dilophodon* and *Desmatotherium* Scott). Premolars $\frac{4}{3}$, the last two in the upper jaw with supplementary crest (metalophid). Upper Eocene (Bridger and Uinta beds); North America.

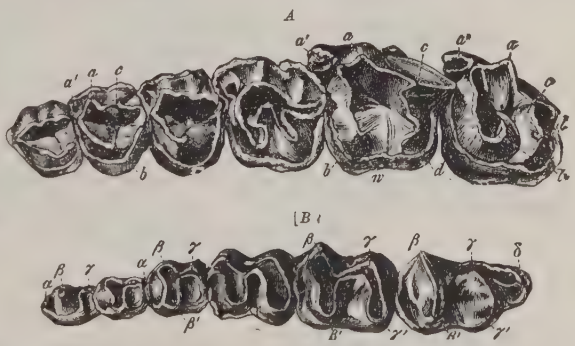


Fig. 168.

Lophiodon isselense Cuvier. Middle Eocene, Issel, Aude. *A*, Left upper cheek teeth. *B*, Left lower teeth. $^1/_2$. (After Filhol.)

Chasmotherium Rütimeyer. Premolars $\frac{4}{4}$, the last two of which are somewhat molariform. Milk cheek

[1] *Filhol, H.*, Études sur les vertébrés fossiles d'Issel. Mém. Soc. Géol. France, 1888.—*Depéret, Ch.*, Études paléontologiques sur les Lophiodons du Minervois. Arch. Mus. d'Hist. Nat. Lyon, t. ix., 1903.—*Stehlin, H. G.*, Die Säugetiere des schweizerischen Eocän. Teil I. Chasmotherium, Lophiodon. Abhandl. Schweizer. Paläont. Gesellsch., 1903.—*Osborn, H. F.*, and *Wortman, J. L.*, Bull. Amer. Mus. Nat. Hist., N.Y., 1892, 1893.

teeth molariform. Third lower molar without third lobe; well-developed cingulum on all teeth. Middle Eocene; France. Bohnerz of Egerkingen and Mauremont.

Lophiodon Cuvier (*Tapirotherium* Blainville) (Fig. 168). Skull low, long, and narrow, gently sloping toward the frontals, with high parietal crest and overhanging occiput. Narial aperture but slightly posterior to the anterior border of the premaxillary. Dental formula: $\frac{3.1.3.3.}{3.1.3.3.}$. Premolars simpler than the molars; last lower molar with a strong third lobe. Enamel very smooth with fine horizontal striae. Manus tetradactyl, the outer digit being only half as long as the others. Metapodials slender. The genus *Lophiodon* is rather widespread in the Lower and Middle Eocene of Europe. More than a dozen species are known, which vary in size between the tapir and the rhinoceros.

Lophiodochoerus Lemoine. Lower Eocene; Rheims, France.

Subfamily 2. Tapirinae.

Lower molars with two transverse ridges standing at right angles to the longitudinal axis of the crown. In forms geologically older, premolars simpler than molars; in later species, molariform.

Fossil in the Eocene, Miocene and Pliocene of North America; in Europe, Oligocene to Pliocene. Pleistocene and Recent in southern Asia and South America.

Systemodon Cope. Dental series nearly continuous. Upper molars with two independently developed and subequal external cones, which are united to the internal cusps by two transverse ridges. The three posterior premolars three-crested, the most anterior small and monocuspid. Lower molars with two transverse crests, last molar with well-developed third lobe. Abundant in the Lower Eocene (Wasatch beds); Wyoming and New Mexico. *S. semihians* Cope.

Fig. 169.

Protapirus priscus Filhol. Phosphorites of Quercy. *A*, Right upper last premolar and molars. *B*, Right lower molars. 1/1. (After Filhol.)

Isectolophus Scott and Osborn. Upper Eocene (Uinta and Bridger beds); North America.

Colodon Marsh. $\frac{3.1.4.3.}{2.1.3.3.}$. Without lower third incisor. Second, third and fourth superior premolars with supplementary crest (metalophid); inferior premolars submolariform, lower third *M* with small third lobe. Metapodials slender. Fifth metacarpal short and tapering. Oligocene; White River beds.

Protapirus Filhol (Fig. 169). Last superior premolar with two external and only one very well-developed internal cusp, the latter apparently resulting from the union of two cones.

Inferior molars with two simple transverse crests occurring at right angles to the longitudinal axis of the crown; third molar without third lobe. Phosphorites of Quercy and Bohnerz of Eselsberg, near Ulm. *P. priscus* Filhol. In the John Day beds of Oregon is found *P. robustus* Sinclair, which is probably generically distinct, as are also *P. obliquidens* Wortman, and *P. simplex* Wortman and Earle, from the Oligocene White River beds of South Dakota.

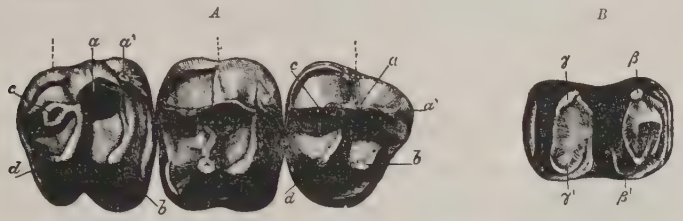


FIG. 170.

Palaeotapirus helveticus, Meyer sp. Lower Miocene (Bohnerz), Eselsberg, near Ulm. *A*, Right upper third and fourth premolars and first molar. *B*, Lower molar. 1/1.

Tapiravus Marsh. Miocene; New Jersey. Pliocene; Rocky Mountains. Very imperfectly known.

Palaeotapirus Gaudry (*Paratapirus* Depéret) (Fig. 170). Premolars (P^1 and P^2) in part simpler than the molars. P^3 and P^4 oblong with two equal crests, upper *M* trapezoidal. Parastyle of the *P* small, of the *M* large. *P.*

FIG. 171.

Skull of *Tapirus bairdius* Gill. Recent, Panama. 1/5.

helveticus Meyer sp. Lower Miocene; Ulm, Mainz; Brüx, Switzerland; Department of Allier and Savoy. *P. yagii* Matsumoto. Miocene; Japan.

Tapirus Linn. (*Elasmognathus* Gill) (Figs. 167, 171). The three upper posterior premolars molariform, but oblong; anterior premolar triangular and tritubercular. Superior canine separated from the first premolar by a long diastema and brought near the incisors. Inferior molars with two transverse crests placed at right angles to the long axis. The two posterior premolars like the molars; the anterior premolar elongate, triangular. Skull with nasal bones very short, pointed in front, and elevated, sometimes supported by a

septum. Manus tetradactyl; pes tridactyl. Now living in South and Central America and East Asia. Fossil tapirs were widespread in the Miocene and Pliocene of Europe: *Tapirus telleri* Hofmann, Upper Miocene of Styria; *T. priscus* Kaup, Lower Pliocene of southern Germany; *T. hungaricus* Meyer, Middle Pliocene of Styria and Hungary; *T. arvernensis* Croizet and Jobert, Upper Pliocene of Auvergne. A gigantic tapir, *Tapirus sinensis* Owen, lived during the Pleistocene in China. In the Pleistocene of North America occurs *Tapirus haysi* Leidy; and *Tapirus tarijensis* Ameghino is known from the Pleistocene of Bolivia.

Family 2. **Rhinocerotidae** Gray.[1]

Nasal bones standing out freely, often with a rugose cushion for one or two horns. Narial openings much prolonged backward. Dental formula: $\frac{3\text{-}0.\ 1\text{-}0.\ 4\text{-}2.\ 3.}{3\text{-}0.\ 1\text{-}0.\ 4\text{-}2.\ 3.}$ *Incisors and canines sometimes wanting. Premolars more or less molariform, less complex only in the oldest forms. Upper molars with thick ectoloph, without a median fold, and with two oblique gently curved transverse ridges intimately connected with the ectoloph. Inferior cheek teeth with two ridges bent at right angles, the posterior of which unites with the protolophid at the antero-external corner. Third molar without talon. Manus with three or four digits.*

To the *Rhinocerotidae* belong chiefly large heavy herbivorous quadrupeds, with a short neck, short legs, and a short tail. They still exist in the low swampy grounds of tropical India, the Sunda Islands, and in Central Africa. The fossil forms appear in the Middle Eocene of Europe and North America, and in the Miocene, Pliocene and Pleistocene had spread over the entire Northern Hemisphere and Northern Africa. They are characterised in part by the presence of stout horns, which originate as true epidermic structures from agglutinated tufts of hair, and are borne on rugose pad-like protuberances of the nasal bone, sometimes also of the frontal bone. If two horns are present, they are usually arranged one behind the other, more rarely side by side (*Diceratherium*).

Only in the earliest types is the dentition complete; in the later forms the canines first become aborted, and afterwards the incisors. In the older forms, either all or the two anterior premolars are much less complex than

[1] *Abel, O.*, Über die paläogenen Rhinocerotiden Europas. Abhandl. k. k. geol. Reichsanst., xx., 1910.—*Brandt, J. F.*, Mém. Acad. Imp. Sci. St-Petersbourg, vol. viii., 1864; vol. xxiv., no. 4, 1877; and vol. xxvi., 1878.—*Cope, E. D.*, On the American Rhinoceroses and their allies. Amer. Nat., p. 770, 1879.—*Douglass, E.*, Rhinoceroses from the Oligocene and Miocene of North Dakota and Montana. Ann. Carnegie Mus., vol. iv., 1908.—*Duvernoy, G. L.*, Nouvelles études sur les Rhinocéros fossiles. Arch. Museum Paris, vol. vii., 1853.—*Flower, W. H.*, On some cranial and dental characters of the existing species of Rhinoceroses. Proc. Zool. Soc. London, p. 443, 1876.—*Hatcher, J. B.*, New fossil Vertebrates. Ann. Carnegie Museum, 1907.—*Meyer, H. von*, Die diluvialen Rhinoceros-Arten. Palaeontgr., Bd. xi., 1864.—*Niezabitowski, L.*, Die Überreste des in Starunia gefundenen Rhinoceros antiquitatis. Bull. Acad. Sci. Cracovie, 1911.—*Osborn, H. F.*, The Extinct Rhinoceroses. Mem. Amer. Mus. Nat. Hist., pp. 79-164, 1898.—Phylogeny of the Rhinoceroses of Europe. Bull. Amer. Mus. Nat. Hist., pp. 229-267, 1900.—*Pavlow, Marie*, Études sur l'histoire paleontologique des ongulés. III. Rhinocerotidae et Tapiridae. Bull. Soc. Imp. Nat. Moscou, 1888; VI. Les Rhinoceridae de la Russie et le developpement des Rhinoceridae en général. *Ibid.*, 1892.—*Peterson, O. A.*, A mounted skeleton of *Diceratherium cooki*. Ann. Carnegie Mus., vol. vii., 1911.—*Weber, M.*, Über tertiare Rhinocerotiden der Insel Samos. Bull. Soc. Imp. Nat. Moscou, 1904, 1905.—*Roman, F.*, Le Caducreotherium. Arch. Mus. Lyon, 1908.—*Toula, F.*, Das Nashorn von Hundsheim. Abhandl. k. k. geol. Reichsanst., 1902, 1906.—*Scott, W. B.*, Osteologie von Hyracodon. Festschr. f. Gegenbaur, 1896.

the molars; in all later rhinoceroses, the premolars and molars, with the exception of the most anterior premolar, exhibit essentially the same composition. Thus, from the transverse ridges of the superior molars (Fig. 172) several folds project into the median valley; according to Osborn's terminology, one from the ectoloph (crista), one from the protoloph (antecrochet), and one from the metaloph (crochet). These folds sometimes unite, enclosing island-like spaces or fossettes. The last inferior molar never has a third lobe.

The skull is low, elongated, occiput surmounted by a sharp occipital crest. The orbits are open posteriorly, and the temporal fossae are unusually large. The nasal bones stand out freely, have very diverse length and stoutness, according as they bear horns or are hornless, and are sometimes supported by a co-ossified mesethmoid. The unusually large narial apertures often extend back as far as the first molar. The well-developed postglenoid process is either separated from the mastoid process (post-tympanic) by a groove or is united with it.

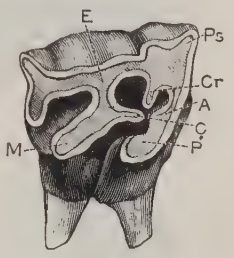


Fig. 172.

Upper molar of *Rhinoceros*. *A*, Antecrochet; *C*, crochet; *Cr*, crista; *E*, ectoloph; *M*, metaloph; *P*, protoloph; *Ps*, parastyle. 1/2.

The extremities are usually short and stout. The radius and ulna are well developed and entirely distinct, as in the tapir. In the older forms, the carpus exhibits nearly the same construction as in the tapir. Of the four metacarpals, the third is stouter than the two adjacent ones, while the fifth is short. In the later forms, the manus has but three toes; the carpals and metacarpals become shorter and broader, and the third metacarpal is considerably stouter than the two lateral metacarpals. The femur is always characterised by a strongly marked third trochanter, situated rather low down on the shaft. In more primitive forms, the tarsus and metatarsus are somewhat elongated and narrow; in more modern types, they are short and broad.

Subfamily 1. Hyracodontinae Cope.

Skull short, with a sagittal crest and with periotic conspicuous laterally. Nasal bones projecting freely, hornless. Dentition complete: $\frac{3.1.4.3.}{3.1.4.3.}$. *Canines weak and immediately following the chisel-shaped incisors, but separated from the cheek teeth by a short diastema. Premolars and molars either heterodont or homoeodont, the superior molars being composed of an ectoloph and two oblique transverse crests, the inferior consisting of two angular crescents, the posterior horn of which forms a transverse crest. Neck long. Extremities long and slender. Manus with three or four digits; pes tridactyl.*

In their general proportions, these slightly built animals, with their long limbs and long and slender neck, bear a far closer resemblance to the horse or *Anchitherium* than to *Rhinoceros*, although the skull and cheek teeth agree more closely in structure with those of the latter genus. They approach the tapirs in the skeleton structure, and form an independent extinct lateral branch of the rhinoceros stem. They are at present known only from the Eocene and Oligocene of North America.

Hyrachyus Leidy (*Colonoceras* Marsh) (Fig. 173). Premolars less complex than the molars, the upper ones trigonodont. Molars short-crowned. Manus tetradactyl, pes tridactyl. Middle Eocene; Bridger beds, Wyoming.

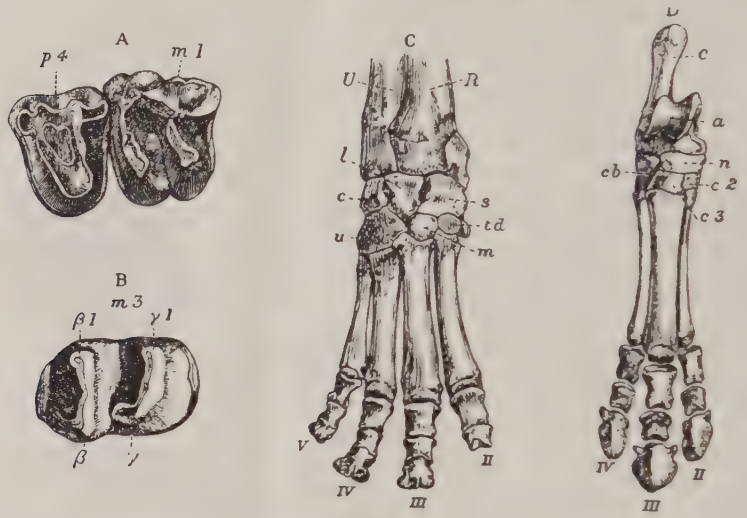


Fig. 173.

Hyrachyus eximius Leidy. Middle Eocene (Bridger beds), Wyoming. *A*, Last upper premolar and first molar. 1/1. *B*, Last lower molar. 1/1. *C*, Right fore-foot. *D*, Right hind-foot. 1/5. (After Cope.)

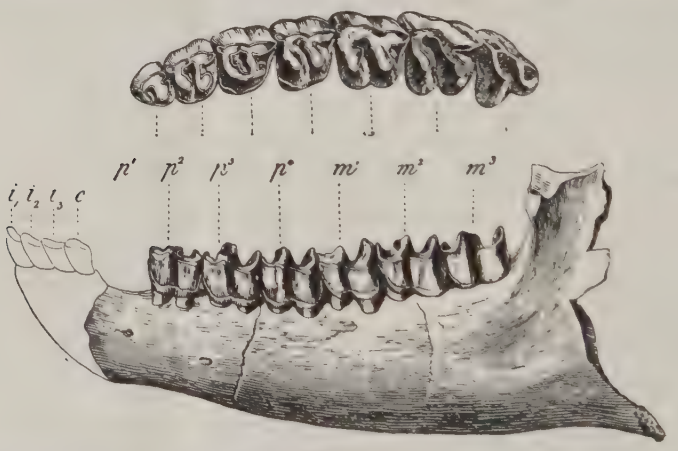


Fig. 174.

Hyracodon nebrascensis Leidy. Oligocene (White River beds), Nebraska. *A*, Upper cheek teeth from below. *B*, Lower jaw from outer side. 1/2.

Triplopus Cope. Molars with higher crowns. Manus tridactyl. Upper Eocene; Wyoming.

Hyracodon Leidy (Figs. 174, 175). Teeth high-crowned. Three posterior

premolars molariform. Manus tridactyl. Oligocene; White River beds, Nebraska and Colorado. *H. nebrascensis* Leidy, *H. major* Osborn.

Subfamily 2. AMYNODONTINAE Scott and Osborn.

Skull deeply excavated in front of the orbits, anterior border of the snout broad, postglenoid process well developed. Nasal bones very short, without horns. Superior and inferior canines peccary-like tusks much more robust than the incisors. Molars like those of Rhinoceros, yet the transverse crests of the superior molars may be either without or with a very weak crochet. Superior premolars less complex or smaller than molars.

FIG. 175.

Hyracodon nebrascensis Leidy. Oligocene (White River beds), Nebraska. Skull. 1/6. (After W. B. Scott.)

Manus tetradactyl, pes tridactyl.

The skeleton of one genus (*Metamynodon*) of these heavy aquatic quadrupeds is well known. The skull, however, more nearly resembles that of the bear than of a perissodactyl. For the most part, these comparatively rare remains come from the Upper Eocene and Oligocene of North America and from the Oligocene of Europe.

FIG. 176.

Metamynodon planifrons Osborn. Oligocene (White River beds), Dakota. Skull. 1/10. (After Osborn.)

Amynodon Marsh (*Orthocynodon* Scott and Osborn). Dental formula: $\frac{3\text{-}2.1.4.3.}{2\text{-}1.1.4.3.}$. Upper Eocene; Wyoming.

Metamynodon Scott and Osborn (Fig. 176). Dental formula: $\frac{2.1.3.3.}{1.1.2.3.}$. Cheek teeth laterally compressed. Crowns of the teeth very high. Oligocene; White River beds, Dakota. According to Pilgrim, also in Burma.

Cadurcotherium Gervais. $\frac{2.1.3.3.}{1.1.2.3.}$. Premolars and molars strongly compressed laterally. Oligocene; Phosphorites, Quercy, Gypsum of Isle-sur-Sorgues.

Subfamily 3. RHINOCERINAE.

Skull elongated, elevated posteriorly, without sagittal crest; occiput surmounted by a sharp occipital crest; periotic not appearing on the outer surface of the skull; nasal bones long, projecting, of diverse strength, with or without horn-pad. Dentition never quite complete. Dental formula: $\frac{3\text{-}0.1\text{-}0.4\text{-}3.3.}{3\text{-}0.\ 0.\ 4\text{-}3.3.}$. *Superior canines nearly always absent; incisors frequently so. Superior first incisor and lower second incisor*

specialised; superior cheek teeth with ectoloph and two oblique transverse ridges; metaloph with crochet, ectoloph usually with crista. Superior and inferior premolars generally molariform. Neck short. Extremities robust. Manus with four or three digits, pes tridactyl.

Fig. 177.

Aceratherium tetradactylum Lartet. Upper Miocene, Sansan (Gers). Left fore-foot. 1/5. (After Blainville.)

All members of this subfamily were included by

Fig. 178.

Aceratherium incisivum Cuvier sp. Lower Pliocene, Eppelsheim. Skull. 1/7. (After Kaup.)

Cuvier in the single genus *Rhinoceros* Linnaeus; now, however, they are separated into a number of genera.

(*a*) *Prohyracodon* Koch. Bones and dentition imperfectly known. Middle Eocene; Transylvania.

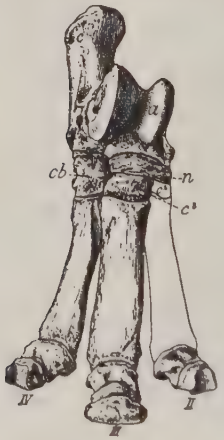


Fig. 179.

Aceratherium sp. Miocene, North America. Right hind-foot. 1/5. (After Osborn.)

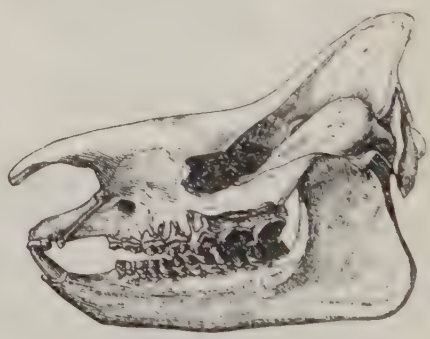


Fig. 180.

Aceratherium tridactylum Osborn. Oligocene (Upper White River beds), Nebraska. Skull. 1/9. (After Osborn.)

(*b*) *Trigonias* Lucas. Dental formula: $\frac{3.1.4.3.}{3.0.4.3.}$. First upper incisor and second lower incisor much larger than the others. Premolars much

simpler than the molars. Narial opening deeply excavated; nasal bones and premaxillaries long. Manus with complete, but much reduced fourth digit. Oligocene; Lower White River beds. *T. osborni* Lucas.

(*c*) *Leptaceratherium* Osborn. Dental formula: $\frac{2.1.4.3.}{2.0.3.3.}$. Premolars somewhat complex. Oligocene; Lower White River beds. *L. trigonodum* Osborn.

(*d*) *Ronzotherium* Aymard. Skeleton not known. Premolars much simpler than molars; those in the lower jaw with incomplete ridges. Superior molars without crista, crochet and antecrochet. Oligocene; Europe. *R. velaunum* Aymard, Ronzon; *R. gaudryi* Rames. In the Phosphorites of Quercy and in the Brown Coal of Bohemia and Piedmont, as well as in the Bohnerz of Swabia, *Rhinocerinae* also occur which probably belong to this genus.

(*e*) *Aceratherium* Kaup (*Caenopus* Cope) (Figs. 177-181). Dolichocephalous. Nasal bones small, projecting freely above the narial openings, hornless;

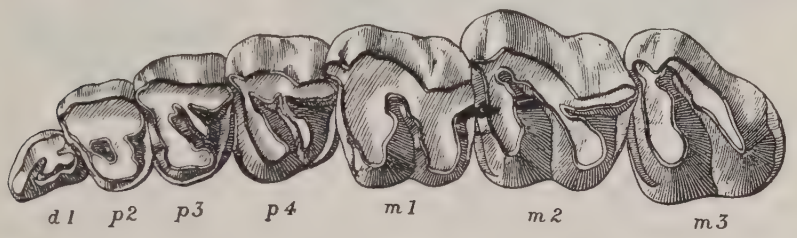


FIG. 181.

Aceratherium platycephalum Osborn. Oligocene (White River beds), Dakota. Left upper cheek teeth. $^1/_2$. (After Osborn.)

frontal bones smooth above; mastoid process (post-tympanic) independently developed and separated from the postglenoid process by a furrow. Dental formula: $\frac{2\text{-}1.0.\ 4.\ 3.}{2\text{-}1.0.4\text{-}3.3.}$. Upper incisors with low laterally compressed crowns elongated antero-posteriorly and with the wear oblique. Lower inner incisors diminutive, deciduous, chisel-shaped; outer very large, procumbent, triangular, with wear posterior. Premolars less complex than the molars. Manus often still tetradactyl, pes tridactyl. To *Aceratherium* belong the earliest representatives of *Rhinoceros*, from the Oligocene Phosphorites of Quercy—*Aceratherium filholi* Osborn. In the Lower Miocene are found *A. lemanense* Pomel (= *R. gannatense* Duvernoy); in the Middle Miocene, *A. platyodon* Mermier; in the Upper Miocene, *A. tetradactylum* Lartet, and *A. zernowi* Borissiak from Sebastopol; and in the Lower Pliocene, *A. incisivum* Cuvier. From the Lower Pliocene of Samos are known *A. samium* and *schlosseri* Weber, the latter nearly allied to *A. blanfordi* Lydekker, occurring in the Siwalik and in China. *A. persiae* Pohlig has been described from Maragha. In the Oligocene of North America (White River beds) are found several species, *A. occidentale* Leidy; *A. tridactylum* Osborn; *A. platycephalum* Osborn and Wortman; *A. mite* Cope.

(*f*) *Diceratherium* Marsh. Dental formula: $\frac{1.0.\ 4.\ 3.}{2.0.4\text{-}3.3.}$. Dolichocephalous.

Each nasal bone usually furnished with a protuberance for the small horns, which are placed side by side. Nearly all premolars molariform. Oligocene; Bohnerz, Europe; *D. zitteli* Schlosser. Lower Miocene; *D. croizeti* Pomel. Middle Miocene; *D. douvillei* Osborn. Upper Miocene; *D. steinheimense* Jäger. One species, also, in the Lower Pliocene. North American Oligocene; *D.*

Fig. 182.

Aphelops megalodus Cope. Lower Pliocene (Loup Fork beds), Colorado. Skull from below. 1/6. (After Cope.)

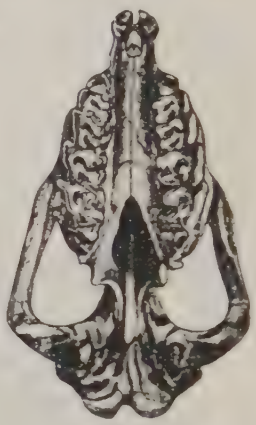


Fig. 183.

Teleoceras fossiger Cope. Lower Pliocene, Kansas. Skull from below. 1/10. (After Marsh.)

proavitum Hatcher. Lower Miocene; John Day beds, *D. armatum* and *nanum* Marsh. Lower Harrison beds, Nebraska, *D. cooki* and *niobrarense* Peterson.

Fig. 184.

Ceratorhinus schleiermacheri Kaup sp. Lower Pliocene, Eppelsheim. Upper molar. 2/3.

(*g*) *Brachypotherium* Roger. $\frac{1.0.4.3.}{1.0.3.3.}$ Brachycephalous. Premolars more simple than molars; all superior cheek teeth very simple, brachyodont with antecrochet only; short diastema in lower jaw. Skull without horn. Extremities short and robust. Middle Miocene; Europe. *B. aurelianense* Noulet. Upper Miocene, *B. brachypus* Lartet. Lower Pliocene, *B. goldfussi* Kaup. *B. perimense* Lydekker from India. *B. pugnator* Matsumoto from Japan.

(*h*) *Teleoceras* Hatcher (Fig. 183) and *Aphelops* Cope (Fig. 182). The first with a small horn at the top of the nasals, the latter hornless. Dental formula: $\frac{1.0.\ 3.\ 3.}{1.0.2\text{-}3.3.}$ Crowns of teeth high; superior molars with well-developed crochet and antecrochet. Brachycephalous. Extremities short and robust. Habit more like *Hippopotamus* than *Rhinoceros*. Upper Miocene and Lower Pliocene, North America, *A. megalodus* Cope. Lower Pliocene, *T. fossiger* Cope.

(*i*) *Ceratorhinus* Gray (*Dihoplus* Brandt) (Fig. 184). Dental formula: $\frac{2\text{-}0.0.4.3.}{1\text{-}0.0.3.3.}$ Upper inner incisor low, with vertically compressed crown, some-

times with an adjacent smaller incisor; inferior incisor small, second incisor triangular, long, horizontal. Cheek teeth brachyodont. Premolars often molariform and superior premolars and molars with crista, antecrochet, and crochet. Brachycephalous. Nasal bones standing out prominently, broad anteriorly, with a rough protuberance for a horn; often a horn on the frontal bone. The older forms possessed incisors that are lacking in later forms; the latter with a bony nasal septum. Lower Miocene, *C. tagicus* Roman. Upper Miocene of Europe, *C.* (*R.*) *simorrensis* and *C. sansaniensis* Lartet; Lower Pliocene, *R. schleiermacheri* Kaup, as well as the existing *C. sumatrensis* Linn., all with incisors. *R. hundsheimensis* Toula, from the older Pleistocene of Lower Austria, probably belongs to *Ceratorhinus*, in which genus also *R. etruscus* Falconer, and *R. mercki* Jäger, referred to *Coelodonta*, could best be placed, notwithstanding the absence of incisors and the presence of a bony nasal septum, for they are doubtless connected genetically with *C. sansaniensis*, etc., while *R. antiquitatis* may be traced back to one of the Pliocene Asiatic species of *Rhinoceros*, probably *R. platyrhinus* Lyd.

FIG. 185.

Atelodus pachygnathus Wagner sp. Lower Pliocene, Pikermi, Greece. Skull. 1/7. (After Gaudry.) *c.oc*, Occipital condyle; *fr*, frontal; *jug*, jugal; *m*, maxilla; *n*, nasal; *oc*, occipital crest; *p.gl*, postglenoid process; *par*, parietal; *tem*, temporal fossa.

FIG. 186.

Coelodonta antiquitatis Blumenb. sp. Pleistocene, Kent's Cavern, Torquay. *A*, Upper molar. 2/3. *B*, Lower molar, inner view. 1/2. (After Owen.)

(*k*) *Rhinoceros* s.str. Gray (*Zalabis* Cope). $\frac{1.0.4.3.}{1.0.3.3.}$ Cheek teeth mainly hypsodont. Nose with but one horn. Occiput inclined forward. Post-tympanic and postglenoid processes anchylosed. Now living in southern India (*R. sondaicus* Horsf.). Fossil in the Siwalik beds, *R. palaeindicus* and *sivalensis* Falconer; Pleistocene of India and Borneo.

(*l*) *Atelodus* Pomel (*Diceros* Gray) (Fig. 185). $\frac{0.0.4.3.}{0.0.3.3.}$ Nose with two horns. Occiput inclined backward; external auditory meatus open below. Premolars molariform. Now living in Africa, *R. bicornis*, Linn. Fossil in the Lower Pliocene, *R. pachygnathus* A. Wagner; Upper Pliocene, *A. morgani* Mecquenem, *R. megarhinus* Christol; and oldest Pleistocene of

Europe, *R. leptorhinus* Cuvier; India, *R. deccanensis* and *karnuliensis* Lydekker; and of China, *R. sinensis* Owen.

(*m*) *Coelodonta* Bronn (Figs. 186-188). $\frac{0.0.4.3.}{0.0.3.3.}$ Nasal bones very well developed, in old forms supported by an ossified mesethmoid. The anterior

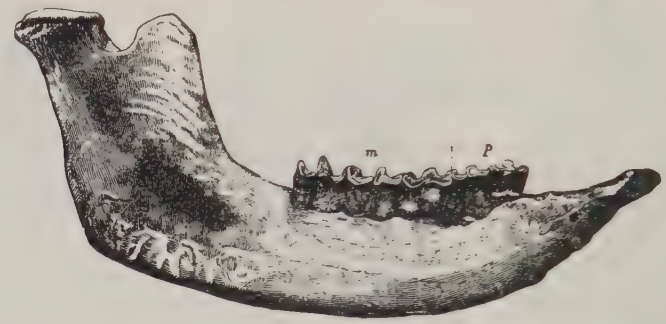


FIG. 187.

Coelodonta antiquitatis Blumenb. sp. Pleistocene, Wirksworth, Derbyshire. Right ramus of lower jaw, outer view. 1/6. (After Owen.)

of the two horns stands on a prominent rough protuberance of the fused nasal bones; the smaller posterior horn, on the frontal bone. In the later Pliocene, *R. etruscus* Falconer, probably a descendant of *R. schleiermacheri*, and in the Pleistocene of North Asia and Europe, *R. mercki* Jäger, in China replaced by *plicidens* Koken, and *R. antiquitatis* Blumenbach (*R.*

FIG. 188.

Coelodonta antiquitatis Blumenb. sp. Pleistocene loess, Kronberger Hof, near Kraiburg, Upper Bavaria. Skeleton, much reduced.

tichorhinus Fischer). Entire carcasses of *R. mercki* and also of *R. antiquitatis*, with skin, hair and well-preserved tissues, have been found in the frozen ground between the Jenisei and Lena rivers in Siberia and in the ozokerite earth of Starunia, Galicia. They were covered with thick woolly hair. The depressions of the cheek teeth contained particles of food, which pertained to conifers and willows. *R. mercki*, however, became extinct in Europe just before the end of the glacial period, while *R. antiquitatis* appeared

later, but continued on into postglacial time. It seems to be allied to *R. platyrhinus.*

Subfamily 4. Elasmotheriinae Gill.

Skull elongated, with tapering pointed snout and much elevated, rugose, hemispherical protuberance on the frontal bone. Nasal bones slender, with a small rough surface on the most anterior portion only. Dental formula: $\frac{0.0.2.3.}{0.0.2.3.}$. *Cheek teeth prismatic, rootless; superior molars composed of ectoloph and two oblique transverse*

Fig. 189.

Elasmotherium sibiricum Fischer. Pleistocene, Siberia. *A*, Skull, lateral aspect. 1/10. *B, C*, Upper and lower molars, crown view. 1/4. (After Brandt.)

crests; inferior molars with two crescents; enamel elaborately crimped. Premolars above and below smaller and somewhat simpler than molars. Skeleton robust. Manus and pes tridactyl.

Elasmotherium Fischer (Fig. 189). *E. sibiricum*, the only species, is found in the older Pleistocene of southern Russia and Siberia; very rarely, also, in Germany.

Sinotherium Ringström. Ancestral to former genus. Pliocene, Shansi, China.

Subfamily 5. Baluchitheriina Osborn.[1]

Head relatively small and neck much elongated, the cervical vertebrae being of very light construction. Skull much elongated, and nasal bones slender without horn. Dental formula: $\frac{1.0.3\text{-}4.3.}{1.0.3\text{-}4.3.}$; *upper incisor caniniform; lower incisor procumbent. Feet much elongated, tridactyl, the middle metapodial longest and stoutest.*

Gigantic long-limbed and long-necked rhinoceroses, found in Oligocene or Miocene formations in Asia. Probably including the largest known land mammals.

[1] *Borissiak, A., Indricotherium*, n.g. Mém. Acad. Sci. Russie [8], vol. xxxv., no. 6, 1923.—*Cooper, C. Forster, Baluchitherium osborni.* Phil. Trans. Roy. Soc. Lond., ser. B, no. 392, 1923. On the Skull and Dentition of *Paraceratherium bugtiense. Ibid.*, no. 399, 1924.—*Osborn, H. F., Baluchitherium grangeri.* Amer. Mus. Novitates, no. 78, 1923. Also Natural History, New York, vol. xxiii., no. 3, 1923.

Baluchitherium Cooper (Fig. 190). Four upper premolars, the first comparatively small and simple. *B. osborni* Cooper, the type species, known by the cervical vertebrae and limb bones from the Lower Miocene of Baluchistan. *B. grangeri* Osborn, known by a skull 1·3 metres in length, from the Upper Oligocene or Lower Miocene of Mongolia. Height of highest part of back about 4 metres.

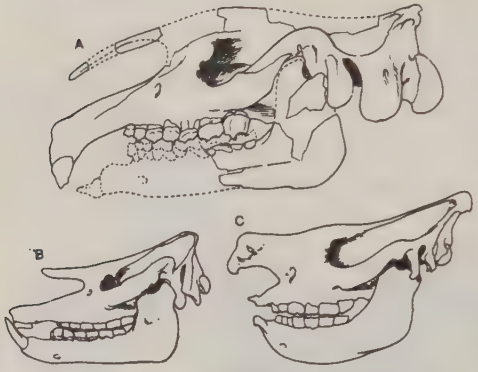


FIG. 190.

Baluchitherium grangeri Osborn. Upper Oligocene or Lower Miocene, Mongolia. *A*, Skull and lower jaw, lateral aspect. 1/22. With skulls and lower jaws of *Aceratherium incisivum* Kaup (*B*), and *Rhinoceros simus* Burchell (*C*) for comparison. (After Osborn.)

(*From a photograph kindly supplied by the American Museum of Natural History, New York.*)

Paraceratherium Cooper. Three upper premolars. Skull less swollen over the frontals than in *Baluchitherium*. Lower incisors sharply conical. *P. bugtiense* Cooper. Lower Miocene, Baluchistan.

Indricotherium Borissiak. *I. asiaticum, I. minus* Boriss. Lower Miocene, Turgai, Turkestan.

Family 3. Equidae Gray.[1]

Nasal bones projecting freely, pointed anteriorly, hornless. Dentition complete. Dental formula: $\frac{3.1.4\text{-}3.3.}{3.1.4\text{-}3.3.}$. *Incisors chisel-shaped. In forms the oldest geologically, premolars less complex than molars; in later species, molariform. Superior molars consisting of two external cusps as a rule joined into an ectoloph, two internal cones, and usually two conical or ridge-like elongated or crescentic intermediate tubercles. The internal and intermediate cusps as a rule connected by ridges. In the most primitive forms, inferior molars quadritubercular; generally, however, composed of*

[1] *Antonius, O.*, Phylogenet. Zusammenhang zwischen Hipparion und Equus. Zeitschr. f. indukt. Abstammungs- und Vererbungslehre, 1919. — *Burmeister, H.*, Die fossilen Pferde der Pampas Formation. Buenos Aires, 1875. Suppl. 1889. — *Cope, E. D.*, Proc. Amer. Philos. Soc., 1889, vol. xxvi. — *Depéret, Ch.*, Revision des Hyracotheridés européens. Bull. Soc. Géol. France, 1901. — *Douglass, E.*, Annals Carnegie Mus., vol. iv., 1908. — *Gidley, J. W.*, Bull. Amer. Mus. Nat. Hist. New York, 1901, 1903. — *Granger, W.*, Bull. Amer. Mus. Nat. Hist. New York, 1906, 1908. — *Huxley, T. H.*, Address delivered at the Anniversary Meeting of the Geological Society. Quart. Journ. Geol. Society, 1870. — *Kovalevsky, W.*, Sur l'Anchitherium et sur l'histoire paléontologique des chevaux. Mém. Acad. St-Pétersb., 1873. — *Forsyth Major, C.*, Beiträge zur Geschichte der Pferde, insbesonders Italiens. Abh. Schweiz. Pal. Ges., vol. iv., 1877; vol. vii., 1880. — *Marsh, O. C.*, Amer. Journ. Sci., 1879, vol. xvii.; 1892, vol. xli. — *Matthew, W. D.*, Suppl. to Amer. Mus. Journ. New York, 1903. — *Matthew, W. D.*, and *Gidley, J. W.*, Bull. Amer. Mus. Nat. Hist. New York, 1906. — *Merriam, J. C.*, Horses of Rancho la Brea; New Protohippine Horses; New Anchitheriine Horses. Univ. California Publ., vol. vii., 1913. New Horses from the Miocene and Pliocene of California. *Ibid.*, vol. ix., 1915. — *Nehring, A.*, Fossile Pferde aus deutschen Diluvialablagerungen. Berlin, 1884. — *Osborn, H. F.*, Equidae of the Oligocene, Miocene, and Pliocene of North America. Mem. Amer. Mus. Nat. Hist., n.s., vol. ii. New York, 1918. — *Reichenau, W. von*, Beitr. Kennt. foss. Pferde aus deutsch. Pleistocän. Abhandl. grossh. hessisch. geol. Landesanst., vol. v., 1915. — *Scott, W. B.*, On the Osteology of Mesohippus. Journ. of Morph., 1891, vol. iii. — *Wortman, J. L.*, Bull. Amer. Mus. Nat. Hist. New York, 1896.

two V-shaped or crescentic ridges opening toward the inside. Manus tetradactyl, tridactyl, or monodactyl; pes tridactyl or monodactyl.

The *Equidae* constitute a family the most abundant in forms, the most highly differentiated in their extremities, and at the same time a very complete genealogy of perissodactyls. They begin in the earlier Eocene and culminate in the existing genus *Equus*. However great the difference may now be between the modern horse and the small tetradactyl ancestral form from the Eocene, the individual genera of the equine series are so closely related to each other that they afford one of the most instructive examples of the gradual modification and specialisation of a definite type of mammalian organisation. The three subfamilies, *Hyracotheriinae*, *Anchitheriinae*, and *Equinae*, merge from one into the other through gradual variations, and represent merely developmental steps in the evolutionary series. Only the fourth subfamily, *Palaeotheriinae*, occupies a separate position. It branched off early from the *Hyracotheriinae*, and after differentiating into a great wealth of species very soon became wholly extinct.

The skull of the *Equidae* is elongated and low; the frontals are broad, and the brain is large and strongly convoluted. The nasal bones are smooth above, hornless and pointed; they project freely above the narial opening, which at times is prolonged far backward, and which is bounded below by the maxillaries and premaxillaries. In the older genera, the orbits are large and wide open posteriorly; in later forms they are smaller and completely surrounded by a ring of bone. The lachrymals are much extended on the face. The postglenoid and paroccipital processes are well developed.

All *Equidae* have above and below on each side three incisors, one canine, and from six to seven cheek teeth. In later forms the enamel of the incisors encloses a depression (mark), which gradually disappears through wear. The diastema between the conical canines and the cheek teeth increases in later genera as a result of the lengthening of the facial bones. The cheek teeth become progressively homoeodont, and at the same time show the gradual modification of the originally short, many-rooted (brachyodont) teeth into the long-crowned prismatic rootless (hypsodont) teeth, which are open below or not closed until late. The superior molars are composed of four main cones, two external and two internal, V-shaped in form, and, as a rule, two intermediate tubercles varying in size and shape. In the oldest genera, the internal and external cusps remain distinct, and only the intermediate tubercles are connected with the internal ones by a slight ridge. In the further development, not only are the external cones united into a continuous W-shaped ectoloph, but likewise the internal and intermediate cusps become modified into oblique and crescentic ridges. The ectoloph has three prominent buttresses, a parastyle in front, mesostyle in the middle, and metastyle posteriorly. The most anterior of the upper premolars is always small and simple; it is never absent in the Eocene genera, yet in later forms it becomes weak and disappears before the last molar breaks through. In the older species, the posterior premolars are tritubercular; in the later ones, molariform. The conformity in the premolars and molars usually takes place earlier in the lower jaw than in the upper jaw. In Owen's figure of *Hyracotherium* the four conical tubercles are either arranged in pairs or alternately opposed to each other, and either remain isolated or are united only by an indistinct transverse crest. (The

actual construction of the teeth is very close to that in *Eohippus*.) In all later *Equidae* the cheek teeth are lophodont. The premolars of the permanent dentition, above and below, always replace three milk teeth; the most anterior milk tooth is not generally succeeded by a premolar. In all *Equidae* the two posterior milk teeth have the structure of the anterior molars, and in the heterodont genera are always more complete than their successors.

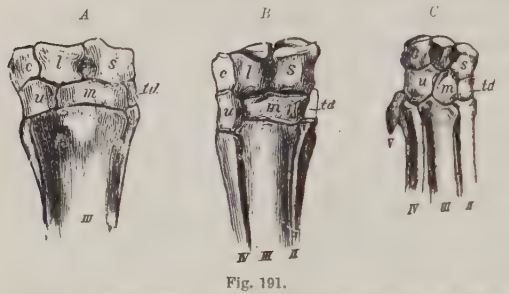


Fig. 191.

Carpus and metacarpus of *Equus* (*A*), *Anchitherium* (*B*), and *Paloplotherium* (*C*), anterior aspect. *c*, Cuneiform; *l*, lunar; *m*, magnum; *s*, scaphoid; *td*, trapezoid; *u*, unciform; *II-V*, metacarpals.

In the oldest forms the extremities are stout; in the later ones they are long and slender. The ossicles of the two carpal series (Fig. 191) alternate with each other. In later forms the magnum, which originally is small, increases much in breadth, pushes the trapezoid inward, and supports the lunar and scaphoid equally. In the more primitive genera four metacarpals are functional. In *Anchitherium*, as a result of the expansion of the magnum,

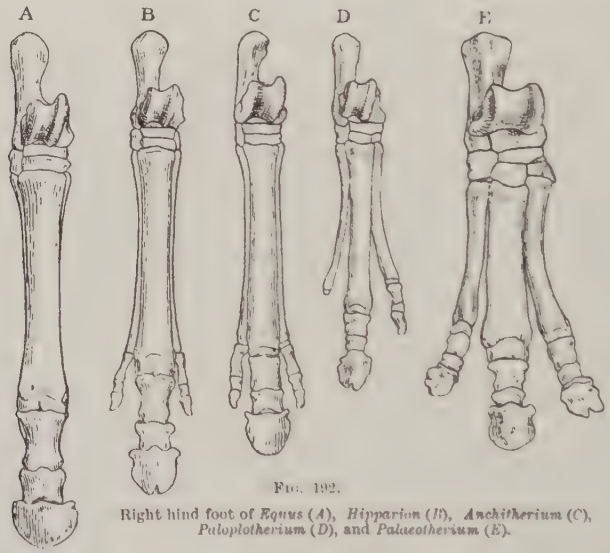


Fig. 192.

Right hind foot of *Equus* (*A*), *Hipparion* (*B*), *Anchitherium* (*C*), *Paloplotherium* (*D*), and *Palaeotherium* (*E*).

the third metacarpal gains a decided superiority over the slender lateral metacarpals, the toes of which, however, still reach the ground. In *Hipparion* and *Protohippus* the metacarpus increases in length, the second and fourth metacarpals are slender, but still reach nearly to the lower end of the exceedingly well-developed third metacarpal, and support short digits which no

longer reach the ground. The fifth metacarpal is only indicated by a small vestigial nodule. In *Pliohippus*, *Equus* and *Hippidium* the two lateral metacarpals finally become reduced to slender tapering splint bones, which in the two last genera reach only just above the middle of the long and stout third metacarpal; the latter alone has three well-developed phalanges, the last of which is encased in a large hoof. The fifth metacarpal has completely disappeared.

The tarsus and hind foot (Fig. 192) undergo a similar modification, so that here also a monodactyl foot with two weak lateral splint bones finally results. The median keels on the distal articular surfaces of the metapodials are at first confined to the posterior side; in the course of time, however, they become more developed, and in the latest genera divide the entire articular surface into two equal parts.

The *Equidae* are divided into four subfamilies: *Hyracotheriinae*, *Palaeotheriinae*, *Anchitheriinae* and *Equinae*.

Subfamily 1. Hyracotheriinae Cope.

Orbits open behind. Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. *Cheek teeth very low, with strong basal cingulum. Premolars usually less complex than molars. Superior molars with four opposite main cones and two smaller intermediate cusps; inferior molars quadritubercular. The upper as well as the lower cusps conical, the upper usually united with a straight ridge, the lower ones united by a* V*-shaped ridge. Radius and ulna distinct, about equally well developed. Manus tetradactyl, pes tridactyl.*

Fig. 193.

Hyracotherium leporinum Owen. Lower Eocene (London Clay), Herne Bay, Kent. *A*, Imperfect skull, palatal aspect. 3/4. *B*, Second upper molar. 2/1. *C*, First lower molar. 2/1. (After Owen.)

The *Hyracotheriinae* are among the oldest and most primitive perissodactyls, and in their dentition have in part retained bunodont characters. The conical external cusps of the superior cheek teeth remain either isolated or are joined to a low ectoloph; the internal and intermediate cones, also, either have no connection with the external cusps or are united with them only by an indistinctly developed band or ridge. The premolars are nearly always less complex than the molars, usually tritubercular. The *Hyracotheriinae* may be derived from the *Condylarthra*, especially from *Tetraclaenodon*, and in their turn are the source of the *Equinae*.

Remains of this subfamily are found only in the Eocene of Europe and North America.

Hyracotherium Owen (*Pliolophus* Owen) (Fig. 193). All cheek teeth

surrounded by a basal cingulum; the cusps either isolated or only indistinctly united by a ridge. Premolars trigonodont. Last inferior molar with single cusped talonid. Lower Eocene; England. *H. leporinum* and *cuniculus* Owen.

Propachynolophus Depéret. Cheek teeth less bunodont than in *Hyracotherium*, with distinct ridges. *P. maldani* and *gaudryi* Lemoine. Lower Eocene; Rheims and Erquellines.

Eohippus Marsh (*Protorohippus* Wortman; *Hyracotherium* Cope) (Figs. 194-196). *M* distinctly lophodont. Upper *P* simpler than *M*. Upper

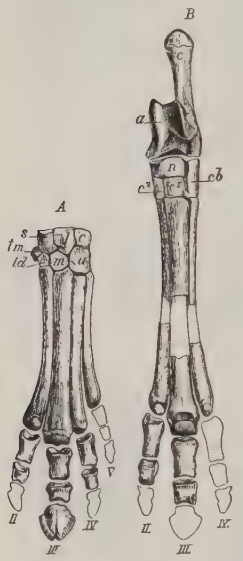


Fig. 194.

Eohippus venticolus Cope sp. Lower Eocene (Wasatch beds), Wyoming. *A*, Left fore foot. *B*, Left hind foot. $^1/_3$. (After Cope.)

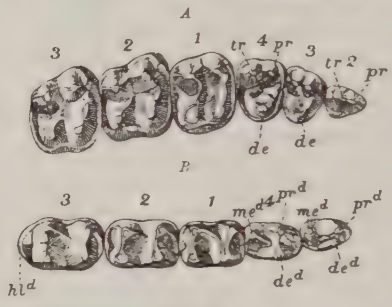


Fig. 195.

Eohippus tapirinus Cope. Lower Eocene (Wasatch beds), Wyoming. *A*, Upper and *B*, lower cheek teeth. $^1/_1$. (After Wortman.)

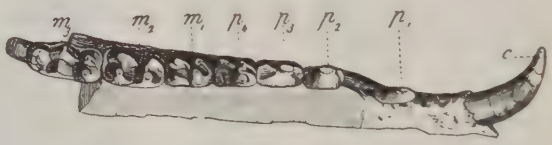


Fig. 196.

Eohippus cristonensis Cope. Lower Eocene (Wasatch beds), Wyoming. Left lower dentition. $^1/_1$. (After Cope.)

molars with subcrescentic external cusps; mesostyle absent and hypostyle weak. Scapula with well-developed coracoid process. Radius and ulna distinct. Fifth metacarpal shorter than the second. Femur with broad third trochanter. Lower Eocene (Wasatch beds); *E. cristonensis, tapirinus, index* Cope, *E. validus* Marsh; Wind River beds, *E. craspedotus, venticolus* Cope.

Orohippus Marsh (*Orotherium, Helotherium* Cope) very similar to *Pachynolophus*. P_4 fully, P^{3-4} partly molariform. Superior molars with hypostyle. Manus tetradactyl. Middle Eocene; Bridger beds, *O. pumilus* Marsh, *O. osbornianus* Cope.

Pachynolophus Pomel. Superior molars with two pyramidal external cusps joined to a moderately arched ectoloph, with a vertical weak mesostyle and parastyle; the two internal cusps conical and subequal. Fourth premolar somewhat lower crowned than first molar, but otherwise similar to it; hypocone distinctly developed. Inferior molars composed of two sharply

bent V-shaped ridges, the inner horns of which, with the exception of the anterior one, rise into pointed cones. Inferior third molar with crescentic talonid. Middle Eocene, France; and Bohnerz, Switzerland. *P. prevosti* Gervais.

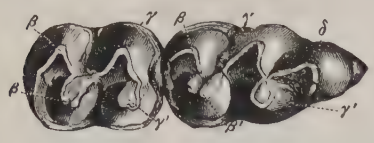


FIG. 197.

Propalaeotherium argentonicum Gervais. Middle Eocene, Argenton, Indre. Two last lower molars. 1/1. (After Filhol.)

FIG. 198.

Propalaeotherium isselanum Gervais. Upper Eocene (Bohnerz), Egerkingen, Switzerland. Upper first molar and two last premolars. 1/1. (After Rütimeyer.)

Lophiotherium Gervais. Upper premolars molariform, sexi-tubercular, with small parastyle and mesostyle on the ectoloph; cusps conical. Lower premolars and molars with angular crescents. Upper Eocene; France and Switzerland. *L. cervulum* Gervais.

Propalaeotherium Gervais (Figs. 197, 198). Superior molars as in *Pachynolophus*. Third and fourth premolars tritubercular, with robust V-shaped internal cone. Inferior cheek teeth consisting of two V-shaped ridges opening toward the inside; the anterior crescent of the first lobe is frequently absent. The two internal cusps rounded, the anterior bilobed. Third molar with well-developed talonid. Premolars less complex than the molars. Middle Eocene; France. *P. argentonicum* Gervais. Also Bohnerz; Egerkingen. *P. isselanum* Cuvier and *P. parvulum* Laurillard.

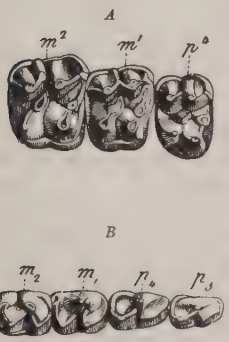


FIG. 199.

Anchilophus desmaresti Gervais. *A*, Upper cheek teeth from Middle Eocene (Calcaire Grossier), Paris. *B*, Lower teeth from Upper Eocene (Bohnerz), Egerkingen, Switzerland. 1/1. (After Kowalevsky.)

Epihippus Marsh. P^3 and P^4 molariform. Manus tetradactyl, third metacarpal enlarged. Upper Eocene (Uinta beds); Wyoming. *E. gracilis* Marsh.

Anchilophus Gervais (Figs. 199, 200). With the exception of the small first lower premolar and P^2 cheek teeth are homoeodont. Diastema between the canine and first premolar long. Upper molars broader than long. Inferior premolars and molars composed of two V-shaped crescents, which meet in a thick bicuspidate internal pillar. Third molar with talonid. Upper Eocene Lignite; Débruge. Phosphorites and Bohnerz. *A. desmaresti* Gervais.

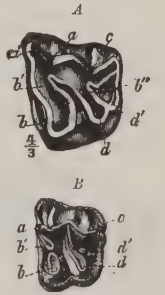


FIG. 200.

A, *Anchilophus desmaresti* Gervais. Upper Eocene (Phosphorites), Quercy. Worn upper molar. 4/3. *B*, *Anchilophus radegondensis* Gervais. Upper Eocene (Bohnerz), Mauremont, Switzerland. Upper molar. 1/1.

Paloplotherium Owen (*Plagiolophus* Pomel) (Fig. 201). Premolars less complex than molars, first premolar usually absent. Upper molars longer than broad. Crowns of the teeth often covered with cement. Extremities

with three long slender toes. Abundant in the Upper Eocene of Europe.

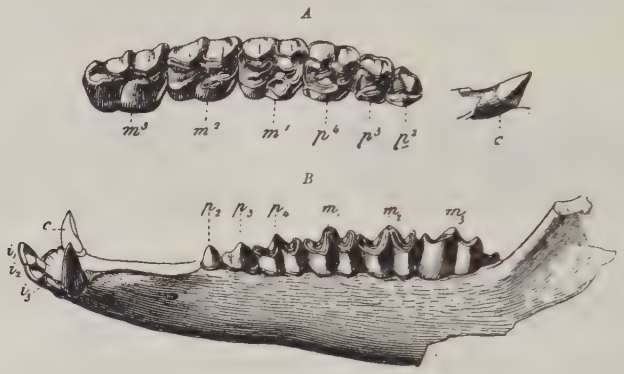


Fig. 201.

Paloplotherium minus Cuvier. Upper Eocene (Lignite), Débruge. *A*, Upper dentition. *B*, Lower dentition. $^2/_3$.

P. annectens Owen. *P. minus* Cuvier. *P. hippoides* Fraas. Rare in the Oligocene of Ronzon, and Bohnerz of Sigmaringen. *P. ovinum* Aymard.

Subfamily 2. Palaeotheriinae Gerard.

Orbits wide open posteriorly. Cheek teeth brachyodont, with several roots. The three posterior premolars molariform in the later species. Superior molars with W-shaped ectoloph and two oblique transverse ridges. The contiguous inner ends of the two crescents of the lower molars form a simple cone. Manus and pes short and robust, tridactyl, the lateral digits reaching the ground and not much more slender than the middle digit. Eocene; Europe.

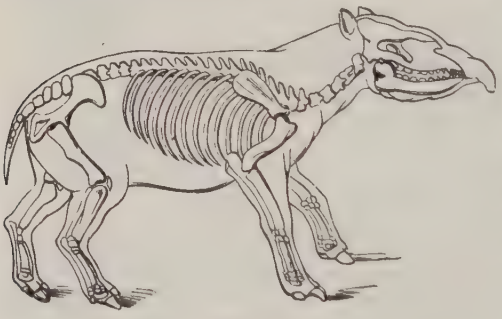


Fig. 202.

Palaeotherium magnum Cuvier. Upper Eocene, Paris. Original restoration by Cuvier.

Palaeotherium Cuvier (Figs. 202-204). Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. With the exception of the small triangular first premolar, superior molars and premolars similar. Ectoloph W-shaped, consisting of two united crescents; internal cusps joined to the ectoloph by oblique transverse ridges. With the exception of the first premolar, inferior cheek teeth composed of two crescents, which at their union form a simple tubercle; third molar with three crescents. Incisors chisel-shaped; canines conical. Carpals rather long and narrow. Of the three metacarpals, which are subequal in length, the median one is but little more robust than the lateral ones. The three digits terminate

in flat distally expanded ungual phalanges. The third trochanter arises somewhat above the mid-length of the femur, and forms a prominent ridge. The three cuneiforms are well developed.

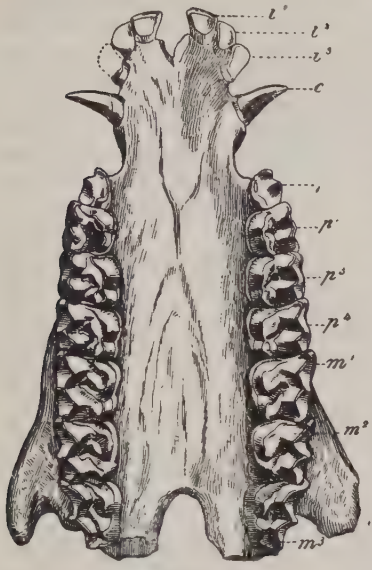


FIG. 203.

Palaeotherium crassum Cuvier. Upper Eocene (Lignite), Débruge. Palatal aspect of skull, showing dentition. 1/4.

Palaeotherium is the dominant form in the Upper Eocene deposits of France, England, southern Germany and Switzerland, and represents the most abundant and characteristic mammalian genus of this horizon. The Paris gypsum has yielded entire skeletons of *P. magnum*, *medium*, and *crassum* Cuvier, while crushed skulls, teeth without number, and isolated bones have been obtained from the lignitic marl of Débruge, near Apt, Vaucluse, as well as from the Phosphorites of Quercy and the Bohnerz of the Swabian and Franconian Alps. The largest species, *P. magnum*, attained the dimensions of a rhinoceros; the smallest, *P. curtum*, at least that of a pig. Middle Eocene. *P. castrense* Nouel; *P. eocaenum* Gervais; *P. rütimeyeri* Stehlin, in part still with simple premolars.

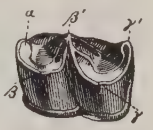


FIG. 204.

Palaeotherium crassum Cuvier. First lower molar. 1/1.

Subfamily 3. ANCHITHERIINAE Leidy

Orbits open posteriorly or incompletely surrounded by bone. Cheek teeth brachyodont. The two or three posterior premolars molariform, rarely all simple. Superior molars with W-shaped ectoloph and two oblique transverse crests and hypostyle. The contiguous internal cusps of the crescents of the inferior cheek teeth form two small cones. Lower M_3 with a small talonid. Radius and ulna usually distinct. Extremities slender, tridactyl, the lateral digits reaching the ground, and much less robust than the middle one.

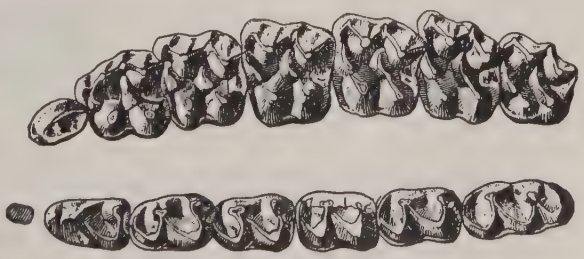


FIG. 205.

Mesohippus bairdi Leidy sp. Oligocene (White River beds), Dakota. Upper and lower cheek teeth. 1/1. (After Osborn.)

Mesohippus Marsh (Figs. 205, 206). Incisors chisel-shaped, without pits. With the exception of the most anterior, cheek teeth homoeodont. Superior

cheek teeth composed of a W-shaped ectoloph, two robust internal cones, and two independently developed intermediate tubercles; also with an accessory intermediate tubercle on the posterior border and hypostyle. The two V-shaped crescents of the inferior cheek teeth form at their union an indistinctly bicuspidate internal pillar. Manus and pes tridactyl, lateral metapodials slender, their toes scarcely reaching the ground. In the forefoot a short splint or styloid vestige of the fifth metacarpal is present. Oligocene (White River beds); S. Dakota, Colorado. *M. bairdi* Leidy sp. has the size of a sheep.

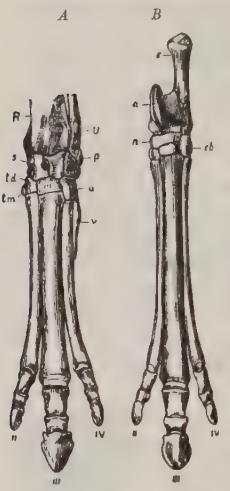


Fig. 206.

Mesohippus celer Marsh. Oligocene (White River beds), Dakota. *A*, Left fore foot. *B*, Left hind foot. 1/3. (After Marsh.)

Miohippus Marsh. Larger than *Mesohippus*, upper incisors with pits, cheek teeth very similar to those of *Mesohippus*. M^3 and heel of M_3 unreduced. Upper Oligocene and Lower Miocene of North America. *M. anceps* Marsh, *equiceps* Cope, *condoni* Leidy, from John Day formation of Oregon; *M. intermedius*, *M. validus* Osborn, from Protoceras beds of South Dakota.

Anchitherium H. von Meyer (Fig. 207). With the exception of the small first lower premolar, cheek teeth homoeodont. Ectoloph of the superior molars and premolars W-shaped. Internal cones robust, united with the narrow intermediate tubercles and with the ectoloph by oblique ridges; accessory intermediate hypostyle (Fig. 207, *d'*) on the posterior border. Crowns of the incisors obliquely inclined inward, with slightly depressed pits. Cheek teeth of the mandible composed of two V-shaped crescents, which at their union form two internal cusps distinct at the tip, connate below; third molar with reduced third lobe. Skull similar to that of *Palaeotherium*. Ulna tapering below and fused with the radius at its slender distal end. Scaphoid and lunar nearly as high as broad, distally both resting on a very broad magnum; unciform narrow and long. Second and fourth metacarpals scarcely one-third as stout as the median one, but little shorter, and bearing three weak phalanges. Fibula extremely slight, styloid, fused with the tibia. Pes tridactyl, lateral metatarsals slender.

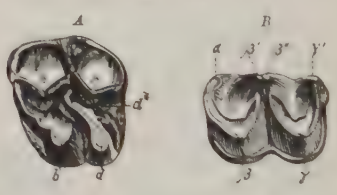


Fig. 207.

Anchitherium aurelianense Cuvier sp. Upper Miocene, Georgensgmünd, Bavaria. *A*, Upper and *B*, lower molar. 1/1.

The single European species, *A. aurelianense* Cuvier sp. (= *Palaeotherium hippoides* Blainville), characterises the Upper Miocene of France, southern Germany and Austria. One species, *A. zitteli* Schlosser, in the Pliocene of China.

Hypohippus Leidy. With brachyodont, Anchitherium-like cheek teeth, and lateral toes very similar. Middle Miocene; Deep River beds, Montana. *H.* (*Anchitherium*) *equinus* Scott. Upper Miocene; *H. affinis* Leidy, *H. matthewi* Barbour. Of larger size.

Parahippus (*Anchippus*) Leidy (Fig. 208). Milk teeth, premolars and molars higher than in *Anchitherium*. Crochet always present. Upper incisors

with pits. Orbits closed posteriorly. Lateral toes shorter than the third. Middle Miocene; Deep River beds, Montana. *P.* "*Desmatippus*" *crenidens* Scott. "*Anchippus*" *brevidens* Marsh. *P. texanus* Leidy. Miocene; Texas. *P. nebrascensis* Peterson. Miocene; Nebraska. Common in the Lower Miocene.

Fig. 208.

Parahippus nebrascensis Peterson. Miocene, Nebraska. Skull and lower jaw. 1/4. (After Peterson.)

Archaeohippus Gidley. Middle Miocene.

Altippus Douglass. Cheek teeth high, second upper premolar elongated. Metapodials very long. Middle Miocene; Montana. *A. taxus* Douglass.

Subfamily 4. Equinae.

Orbits completely surrounded by bone. Cheek teeth hypsodont, with nearly always copious cement. First premolar very small, weak, often absent; other premolars molariform. Superior molars with elongated crescentic intermediate tubercles, which form closed pits. First inner cusp large, developed as basal pillar, second small. Inferior premolars and molars with large internal pillar developed as a double loop at the point of union of each crescent. Incisors chisel-shaped, the enamel on the crown infolded and forming a pit. Radius and ulna anchylosed together, the latter very slender at the distal end. Manus and pes tridactyl or monodactyl, lateral metapodials rudimentary, either with short phalanges or reduced distally to tapering splint bones.

Fossil in the Pliocene and Pleistocene of Europe, Asia, northern Africa and North America, occurring also in the Middle and Upper Miocene of the latter continent. In South America only in the Pleistocene, and at present distributed over the whole earth, but indigenous only in Europe, Asia and northern Africa.

Merychippus Leidy (Fig. 209). Milk teeth brachyodont with little cement; premolars and molars moderately hypsodont with abundant cement. Enamel of the upper teeth more or less infolded. Middle Miocene to Lower Pliocene; North America. *M. insignis* Leidy. *M. sejunctus* Cope sp.

Protohippus Leidy (Figs. 210, 211, *D*). Protocone of the upper molars joined to the protoconule. Folding of the enamel very slight. Cement copious. Inferior molars as in *Equus*, but lower. Without lachrymal fossa. Manus and pes tridactyl, the lateral metacarpals and metatarsals very slender, the toes not reaching the ground, as in *Hipparion*. Low Pliocene (Loup Fork beds); North America. *P. perditus, placidus, mirabilis* Leidy. Pliocene, *P. cumminsi* Cope.

Pliohippus Marsh. A doubtful genus. Malar and lachrymal fossa large. Teeth very similar to those of *Protohippus*. Lateral metapodials sometimes without phalanges. Lower Pliocene (Loup Fork beds); North America. *P. pernix, P. robustus* Marsh.

Hipparion Christol (*Hippotherium* Kaup) (Figs. 211, *B*; 212, 213). Incisors

with pits. Canines present in both sexes. Cheek teeth prismatic, but only half as deep as in the horse. First superior premolar small, early deciduous;

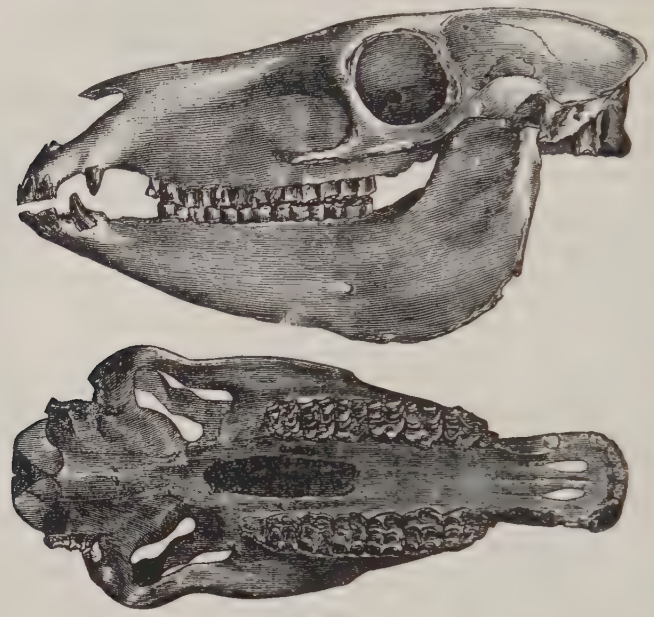


Fig. 209.

Merychippus sejunctus Cope sp. Lower Pliocene, Colorado. Lateral aspect of skull and lower jaw, and palatal aspect of skull. 1/3. (After Cope.)

second premolar broadly triangular, somewhat larger than the other cheek teeth. Protocone forming an isolated cylindrical pillar. Enamel of the valleys strongly wrinkled; cement very abundant. Inferior molars consisting of two crescents, which through their union form one longitudinal double column; this through wear is represented by large plications. The internal horn of the hypolophid also develops into an oblong column, which sometimes comes in contact with the metastylid. The milk teeth resemble the succeeding premolars, yet are somewhat more elongate, lower and with longer roots. The inferior milk teeth are characterised by a very small pillar in the median transverse valley of the external side; the superior milk teeth are narrower than their successors and less copiously filled with cement. Skull somewhat smaller and lower than in the horse. In front of the lachrymal is a deep fossa bounded below by the broad maxillary crest. Extremities tridactyl, the median metapodial

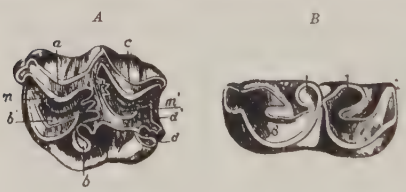


Fig. 210.

Protohippus mirabilis Leidy sp. Lower Pliocene, Nebraska. *A*, Upper milk-molar. *B*, Lower molar. 1/1. (After Leidy.)

very stout, with a well-developed keel on the distal articular surface; lateral metapodials slender, with short digits not reaching the ground.

The genus *Hipparion* is distinguished from the horse by its more delicate structure, smaller size (being intermediate between the ass and the zebra in

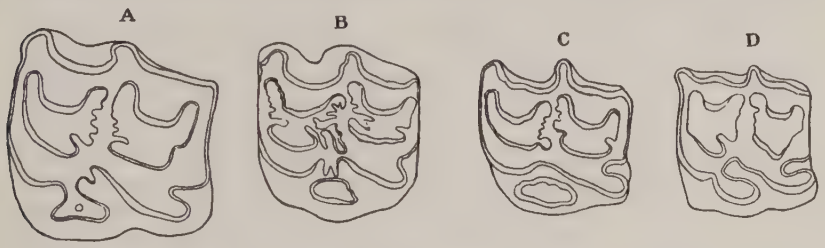


FIG. 211.

Upper molar of *A*, *Equus stenonis* Cocchi. *B*, *Hipparion gracile* Kaup sp. *C*, *Neohipparion dolichops* Matthew. *D*, *Protohippus* sp.

this respect), by the anomalous character of its upper cheek teeth, and especially by its tridactyl feet. In Europe it characterises the Lower and Middle Pliocene deposits; it probably lived in great herds, and left behind numerous remains at Eppelsheim, Hesse-Darmstadt; at Mont Lebéron, Vaucluse; Concud, Spain; Baltavár, Hungary; Pikermi, near Athens; Samos, and elsewhere. *H. gracile* Kaup, *H. mediterraneum*, *H. brachypus* Hensel. Middle Pliocene; Perpignan. *H. crassum* Gervais. In China, *H. richthofeni* Koken; in the

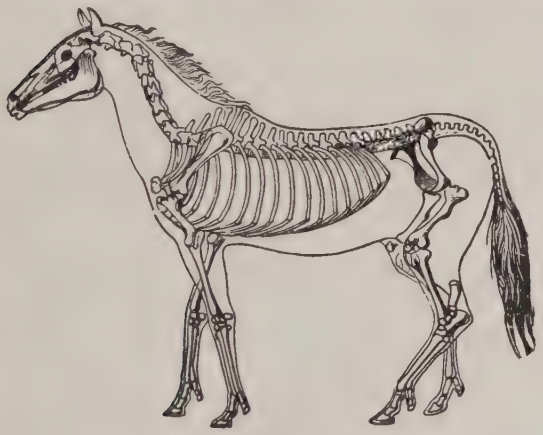


FIG. 212.

Hipparion gracile Kaup sp. Lower Pliocene of Europe. Restoration of skeleton.

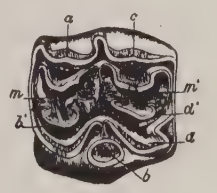


FIG. 213.

Hipparion gracile Kaup sp. Lower Pliocene, Pikermi, near Athens. Upper molar, showing separate inner column (*b*). $^1/_1$.

Siwalik, *H. theobaldi* Lydekker, and *H. antilopinum* Falconer. *Hipparion* is also known from Algiers, Egypt and Persia. In southern Russia and in Samos the small *Hipparion minus* Pavlow, together with *H. gracile*.

Neohipparion Gidley (Fig. 211, *C*). Dentition like that of *Hipparion*, but in some species the protocone of the superior cheek teeth, instead of being cylindrical, is elliptical, and often even concave externally. In the typical species *N. whitneyi*, the folding of the enamel is less marked, the ectoloph of the external cusps is distinctly concave, the external pillar of the inferior

milk teeth is elliptical in cross-section, the bones of the extremities, especially the metapodials, are more slender, and the lateral digits are more strongly reduced. *Neohipparion* is probably confined to the Upper Miocene. *N. occidentale* Leidy, Nebraska. *N. whitneyi* Gidley, South Dakota; *N. speciosum* and *N. gratum* Leidy, Nebraska.

Hippidium Owen (*Rhinippus* Burmeister). Dentition very similar to that of *Protohippus*, but without wrinkling of the enamel, yet the superior cheek teeth are strongly curved, shorter than in *Equus*, with separate roots closed below; the two internal tubercles subequal in size, oval, united with the crescentic intermediate pillars. Narial aperture extending back to above the last molar; nasal bones unusually long, projecting freely. Metapodials stouter and shorter than in the horse; lateral splint bones reaching to just above the mid-length of the median metapodial. Lower Pampas formation; Argentina, Brazil and Bolivia. *H.* (*Equus*) *neogaeum* and *H. principale* Lund sp. *Onohippidium* Moreno, with long deep pit in front of the lachrymal. Pleistocene; Argentina.

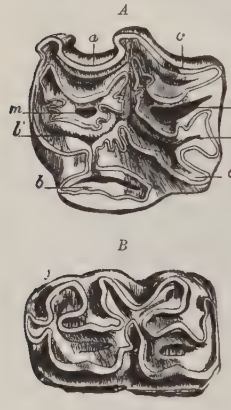


FIG. 214.

Equus caballus Linn. Pleistocene and Recent. *A*, Upper molar, showing inner column (*b*). *B*, Lower molar. 1/1.

Equus Linn. (Figs. 211, *A*; 214). Incisors with pit. Cheek teeth much deepened, prismatic, in the young open below, without separate roots. First premolar in the upper jaw very small, peg-shaped, rarely present. In the superior molars, the infolding of the enamel of the intermediate cusps less elaborately crimped than in *Hipparion*. Both internal cones connected with the intermediate tubercles by a narrow neck; protocone considerably more robust than hypocone and usually elliptical. Cement very copious. Inferior cheek teeth as in *Protohippus*, but much higher crowns. In the carpus, the trapezium and fifth metacarpal are absent. The lateral metapodials of both manus and pes are represented by styloid splint bones without digits; however, abnormal individuals are sometimes found in which the splint bones are well developed and bear three phalanges, as in *Hipparion*. On the other hand, the cases described as atavistic by Marsh are merely abnormalities, like the supernumerary sixth digit in man. They are so proved to be by the presence of two *ossa magna*.

The genus *Equus* had its inception in India, in the Lower Pliocene? (Siwalik beds), and in China, originating in *E. sivalensis* Falconer; in Europe, in the Upper Pliocene, in *E. stenonis* Cocchi, also in the oldest Pleistocene of Mosbach, followed by *E. süssenbornensis* Wüst. In the Pleistocene of India it is represented by *E. namadicus* Falconer. In the later Pleistocene (Diluvium) throughout Europe, northern Asia, and northern Africa, *E. caballus* Linn. is exceedingly widespread, while the Dzeggetai, *E. hemionus*, only occasionally occurs, and the existence of the ass, *E. asinus*, remains doubtful. In North America, the genus *Equus* first appears in the so-called "Equus beds" of the western and southern states, as well as Mexico, and has become differentiated into a considerable number of species in the Lower Pleistocene; *E. intermedius* Gidley. It continued on into the Middle Pleistocene; *E. complicatus* Leidy, *E. crenidens* Cope, *E. scotti* Gidley, *E.*

fraternus, *E. occidentalis* Leidy, etc. Yet became wholly extinct in the present geological period, and was again introduced on this continent through European colonists. In South America, also, several species of *Equus* are distributed through the Middle and Upper Pampa formation and later Pleistocene; *E. curvidens* Owen, *E. andium* Wagner. To the taming and domestication of the Old World wild horse, which probably began in the oldest Stone Age, is to be ascribed the later division of the domestic horse into numerous races.[1]

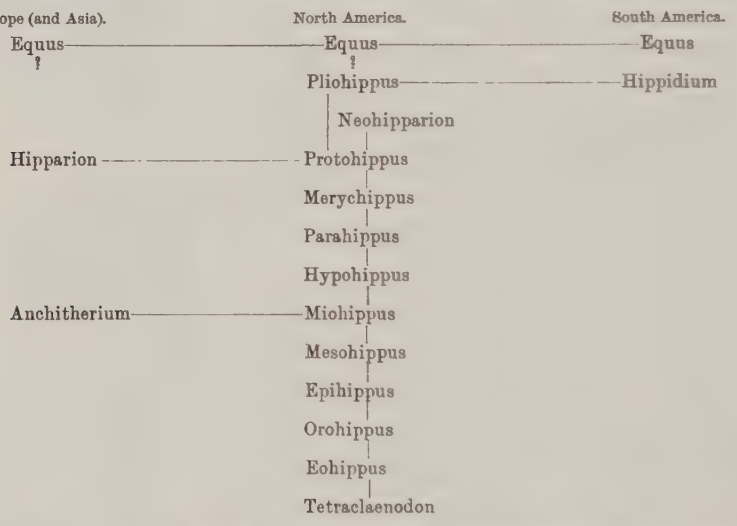
GEOLOGICAL DISTRIBUTION AND PHYLOGENY OF THE EQUINE MAMMALS.

	North Africa.	Europe.	Asia.	North America.	South America.
Recent	Equus	Equus	Equus	Equus (introduced from Europe)	Equus (introduced from Europe)
Pleistocene (Diluvium)	Equus	Equus	Equus	Equus	Hippidium Equus
Upper Pliocene		Equus	Equus Hipparion Anchitherium	Protohippus Pliohippus Merychippus	
Middle Pliocene	Hipparion	Hipparion			
Lower Pliocene		Hipparion			
Upper Miocene		Anchitherium		Neohipparion Merychippus	
Middle Miocene		Anchitherium		Merychippus Parahippus Hypohippus	
Lower Miocene				Mesohippus Miohippus	
Oligocene		Paloplotherium Palaeotherium		Mesohippus Miohippus	
Upper Eocene		Paloplotherium Anchilophus Lophiotherium Palaeotherium		Epihippus	
Middle Eocene		Palaeotherium Propalaeotherium Pachynolophus Hyracotherium		Orohippus	
Lower Eocene		Propachynolophus Hyracotherium Pleuraspidotherium ?		Eohippus	

[1] *Ewart, J. Cossar*, The Multiple Origin of Horses and Ponies. Trans. Highland and Agric. Soc., Scotland, 1904. Skulls of Horses from Roman Fort at Newstead, near Melrose. Trans. Roy. Soc. Edinb., vol. xlv., No. 20, 1907.—*Hernandez-Pacheco, E.*, Los Caballos del Cuaternario Superior segun el Arte Paleolitico. Madrid, 1919.

Various hypotheses have been advanced concerning the ancestry of the horse and of other genera of the *Equidae*. Cuvier early directed attention to the relationship of *Palaeotherium* and *Equus*; Huxley determined that *Equus*, *Hipparion*, *Anchitherium* and *Paloplotherium* (*Plagiolophus*) were developmental stages in an evolutionary series, in which Kowalevsky substituted *Palaeotherium medium* for *Paloplotherium*. The gradual modification of the equine foot and dentition was also so thoroughly worked out by Kowalevsky, that the pedigree of the horse with the stages above mentioned seems established. The discovery of numerous genera in North America furnished still further evidence of the ancestry of the *Equidae*. Marsh showed that the latter continent contained a far more nearly complete series of evolutionary stages, and that the modern horse probably originated in the New World, not in Europe.

According to the present state of knowledge, the following genealogical table may most nearly represent the pedigree of the *Equidae*:



The European genera *Paloplotherium*, *Palaeotherium*, *Propalaeotherium*, *Anchilophus*, *Lophiotherium*, and *Pachynolophus* are without importance for the phylogeny of the true horses. They all appear nearly at the same time, and become extinct simultaneously. Their common ancestor seems to be a *Hyracotherium*.

Family 4. **Titanotheriidae.**[1]

Nasal bones projecting freely, smooth or furnished with two obtuse conical bony protuberances. Orbits open posteriorly. Dental formula: $\frac{3\text{-}0.1.\ 4.\ 3.}{3\text{-}0.1.4\text{-}3.3.}$. *In later*

[1] *Douglass, E.*, Titanotheres from Uinta Deposits. Annals Carnegie Mus., vol. iv., 1911.—*Earle, C.*, A memoir upon the genus Palaeosyops. Journ. Acad. Nat. Sci. Philad., 1892, vol. ix.—*Hatcher, J. B.*, Cranial Elements of Titanotherium. Annals Carnegie Mus., 1901.—Amer. Naturalist, 1895, p. 1084.—*Marsh, O. C.*, Amer. Journ. Sci., 1876, vol. xi.; 1889, vol. xxxvii.; 1890, vol. xxxix.—*Osborn, H. F.*, Bull. Amer. Mus. Nat. Hist. New York, 1902, 1908, 1913.

forms, incisors small, weak; in older species, very well developed. Diastema between canines and premolars very short. In older forms, all premolars less complex; in later species, the two posterior premolars more complex. Superior molars with W*-shaped ectoloph and two conical internal cusps; inferior molars consisting of two* V*-shaped crescents, the inner horns of which at their union usually form a bicuspidate pillar. Third lower molar with large third lobe. Manus tetradactyl: pes tridactyl. Hoofs moderately broad, flattened below.*

This wholly extinct family, which was limited principally to the Eocene and Oligocene of North America, includes large robust ungulates that in external appearance chiefly recall the tapir and rhinoceros, but sometimes nearly equalled the elephant in size. As their dentition indicates, they fed on succulent vegetation. The cheek teeth have very low crowns; the two external cusps of the superior molars are V-shaped, and through their union form a W-shaped ectoloph with a parastyle and mesostyle. The two conical

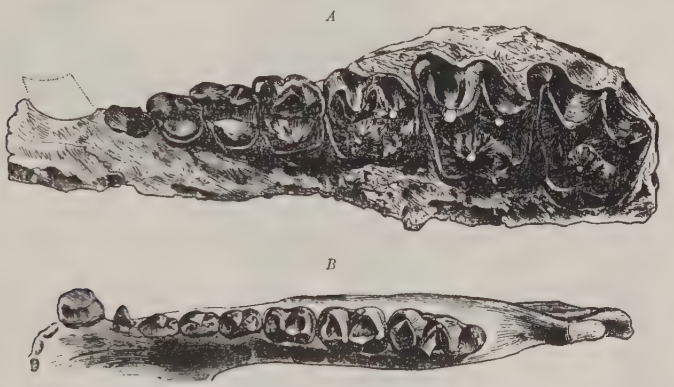


FIG. 215.

Palaeosyops major Leidy. Middle Eocene (Bridger beds), Green River, Wyoming. *A*, Upper cheek teeth. *B*, Lower jaw. 1/3.

internal cusps generally remain distinct or are joined to the ectoloph by a slight ridge; the protocone is always stouter than the hypocone. The superior canines are only moderately robust and either immediately follow the cheek teeth or are separated from them by a very short diastema. The Eocene genera have the full number of incisors, but in Oligocene forms these teeth are deciduous.

The posterior premolars are distinguished from the molars by their smaller size and less complex construction; the two anterior premolars are somewhat simpler. With the exception of the first, all the cheek teeth in the mandible are composed of two V-shaped crescents. The skull is elongated and low; the brain-cavity is small. In later forms, blunt conical bony protuberances arise on the posterior border of the nasal bones; these probably differ in size in the male and female. The extremities are similar to those of the tapir. The carpus is broad and the ossicles of both series really alternate, although there is very little lateral displacement. The manus has four functional digits; the pes, three. The calcaneum presents a facette for the fibula. The ungual phalanges are flattened distally and somewhat expanded.

Subfamily 1. Palaeosyopinae Osborn.

All premolars less complex than molars. Three (rarely two) conical incisors in each ramus of the jaw. Canines large. Eocene; North America and Europe.

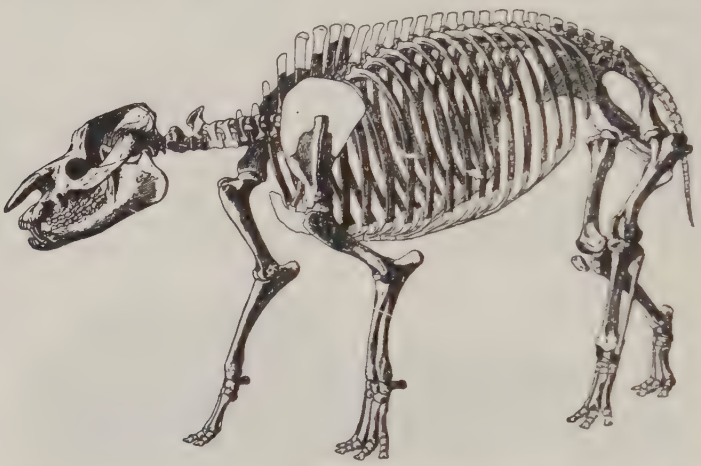


Fig. 216.

Palaeosyops paludosus Leidy. Eocene of North America. Restoration of skeleton. $\frac{1}{16}$. (After Earle.)

Lambdotherium Cope. Extremities slender. Lower Eocene; Wyoming. This genus connects the *Titanotheriidae* with the other perissodactyls.

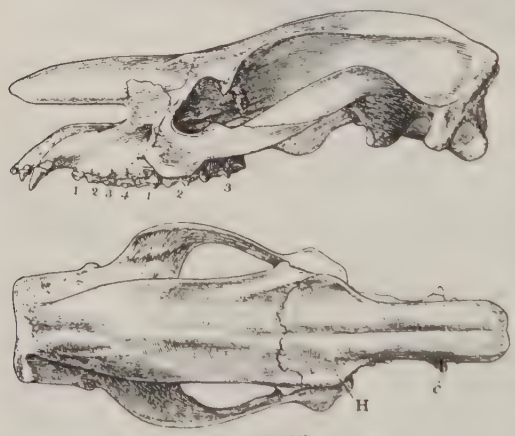


Fig. 217.

Telmatherium cornutum Osborn. Upper Eocene (Uinta beds), Wyoming. Skull in lateral and superior aspects. *H*, rudiment of nasal horn-core; *c*, canine tooth. $\frac{1}{8}$. (After Osborn.)

Palaeosyops Leidy (*Limnohyus* Marsh). (Figs. 215, 216). Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. Canines long and pointed. Superior premolars trigonodont. Manus tetradactyl; pes tridactyl. Abundant in the Wind River and Bridger formations (Eocene) of North America. *P. major, paludosus* Leidy, etc.; one species, also, in the Uinta beds.

Limnohyops Marsh. Eocene. *L. laticeps* Marsh. *Manteoceras* Osborn.

Telmatherium Marsh (Fig. 217). Skull flat; nasal bones long, with bony protuberances on the naso-frontal border. Upper

Eocene; North America. *T. megarhinum* Earle. According to Pilgrim, also in Burma.

Mesatirhinus and *Mesarhinus* Osborn. With narrow skull. Eocene.

Dolichorhinus Osborn. Skull elongated, with long muzzle. Eocene.

Diplacodon Marsh. Nasal bones short, often with two lateral bony protuberances. Extremities robust. Upper Eocene; Uinta beds.

Brachydiastematherium Boeckh and Maty. Only lower jaw known. Middle Eocene; Transylvania.

Subfamily 2. TITANOTHERIINAE Osborn.

Dental formula: $\frac{2\text{-}0.1.\ 4.\ 3.}{2\text{-}0.1.3(4).3.}$. *Dentition in a continuous series. Milk*

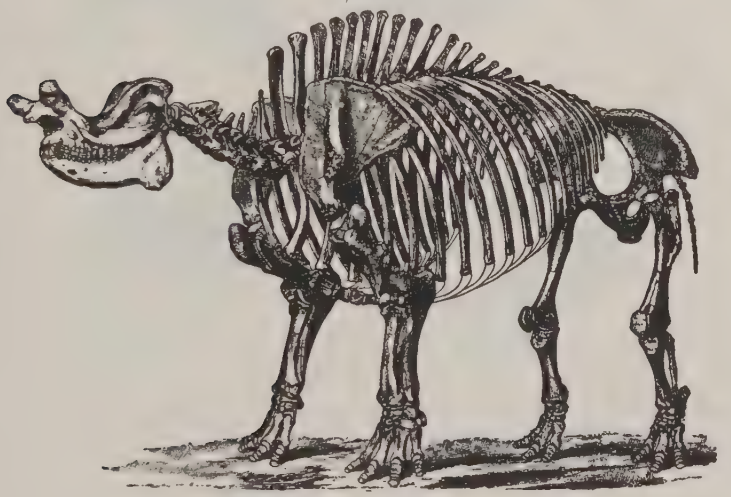


FIG. 218.

Megacerops (*Brontops*) *robustus* Marsh sp. Oligocene, Dakota. Restoration of skeleton, about 1/40. (After Marsh.)

dentition: $\frac{2.1.4.}{2.1.4.}$. *Incisors small, occurring in varying numbers, sometimes rudimentary or absent. Canines conical, generally small. Premolars and molars similar. Naso-frontal border with a pair of well-developed obtuse bony prominences, which in late members of this group may attain huge dimensions, as in Symborodon and Brontotherium. Manus with four digits, pes tridactyl.* Oligocene; North America. One very imperfectly preserved species, also, in Europe.

These enormous animals have a height of nearly two and one-half metres, and are only a little smaller than the elephant. Entire skeletons, numerous skulls, and a great abundance of other remains have been found in the White River beds (Lower Oligocene) of Nebraska, Dakota, and Colorado.

Titanotherium Leidy (*Palaeotherium* Prout; *Menodus* Pomel; *Brontotherium*, *Menops* Marsh) (Fig. 220), derived from *Diplacodon*; *Megacerops* Leidy (*Brontops*

Marsh) (Figs. 218, 219), derived from *Palaeosyops*; *Allops* (*Diploconus*) Marsh, *Symborodon* Cope, and *Brontotherium* (*Titanops*) Marsh.

FIG. 219.

Megacerops (*Brontops*) *dispar* Marsh sp. Oligocene, Dakota. Skull in superior and lateral aspects. 1/8. (After Marsh.)

Protitanotherium Hatcher. Known by the lower jaw of a gigantic form. Upper Eocene (Uinta beds); Utah.

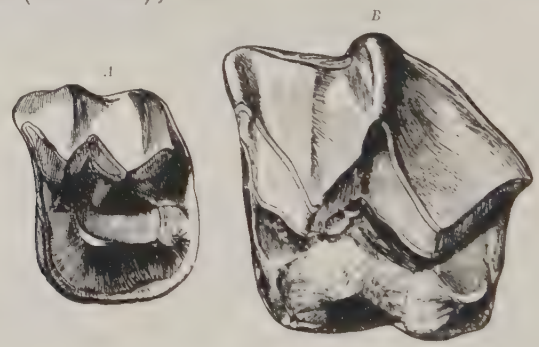


FIG. 220.

Titanotherium prouti Leidy. Oligocene, Dakota. *A*, Last upper premolar. *B*, Second upper molar. 2/3.

Toula has described, as *Menodus rumelicus*, some Titanotherioid teeth from Rumelia, the geological age of which is not yet known.

Family 5. Chalicotheriidae Gill.[1]

Dentition: $\frac{?\ 0.\ 3.3.}{3\text{-}0.1\text{-}0.3.3.}$; *bunolophodont; premolars less complex than molars, superior ones with only one internal and one external cone. Superior molars with* W*-shaped ectoloph and two unequally large conical internal cusps. Inferior molars with two* V*-shaped crescents.* M_3 *without third lobe. Long diastema between cheek and front teeth. Skull ranging from brachycephalic to dolichocephalic. Auditory bulla present. Orbit open posteriorly. Pelvis elongated (Moropus). Third trochanter prominent or wanting. Fore and hind limbs subequal in length or fore limbs longer than hind limbs. Fore feet tetradactyl, afterwards tridactyl. Distal face of astragalus articulating with the navicular and cuboid, or with the navicular only. Distal ends of metapodials with highly convex dorsal articulation for proximal phalanx, or carnivore-like. Terminal phalanges high, laterally compressed, pointed, and deeply bifid.* Tertiary; Europe and North America. Pliocene of India and China. Pleistocene; Uganda.

This family was formerly placed in the order *Ancylopoda*, in which were also included the *Homalodontotheriidae*. The latter, however, are now considered referable to the suborder *Entelonychia*, limited exclusively to South America, and exhibiting merely a similar differentiation of the terminal phalanges, which are clawlike as in the *Chalicotheriidae*. This latter family must be referred to the perissodactyls, among which, in the structure of their teeth, they are most closely allied to the *Titanotheriidae*, while some cranial characters are suggestive of the *Equidae*. The Chalicotheres are distinguished from all typical perissodactyls by a number of highly characteristic features, among which may be mentioned the curiously carnivore-like humerus, the sharply pointed, claw-like, and cleft terminal phalanges, and the carnivore-like convexo-concavity between the metapodials and the proximal phalanges. By means of the latter modification the second digit of the manus is capable of great dorsal flexion. The carpus, on the other hand, is strongly interlocking as in the perissodactyls, while the astragalus of the pes sometimes articulates as in the latter, that is, with navicular and cuboid (*Macrotherium*), or with the navicular only (*Moropus* and *Nestoritherium*). The remains indicate that the animals varied in size from less than half that of an American tapir to larger than a rhinoceros. In the memoir of Holland and Peterson three subfamilies are proposed as follows:—

Subfamily 1. Schizotheriinae.

Manus tetradactyl with vestigial pollex (Schizotherium); manus and pes less specialised than in later forms (especially in Eomoropus of North America).

Schizotherium Gaudry (*Limognitherium* Gervais). Established on fragments of the maxillary with premolars and two anterior molars; metatarsals, metacarpals and phalanges associated. Dentition $\frac{?\ ?\ 3.3.}{?\ ?\ 3.3.}$. Upper molars longer

[1] *Abel, O.*, Lebensweise von Chalicotherium. Acta Zoologica (Stockholm), vol. i., 1920.—*Barbour, E. H.*, Moropus. Nebraska Geol. Surv., vol. iii., 1908.—*Depéret, C.*, Arch. Mus. Hist. Nat. Lyon, vol. v., 1892.—*Filhol, H.*, Mammifères de Sansan. Ann. Sci. Géol., vol. xxi., 1891.—*Osborn, H. F.*, Eomoropus. Bull. Amer. Mus. Nat. Hist., 1913.—*Peterson, O. A.*, Amer. Naturalist, 1907.—*Holland, W. J.*, and *Peterson, O. A.*, Mem. Carnegie Mus., vol. iii., No. 2, 1914.

than broad; trapezium present; facet for vestigial pollex; Mc. II. and IV. long when compared with later forms (*Moropus*); Mc. V. present; Mt. III. and IV. subequal in length. Quercy Phosphorites; France.

Pernatherium Gervais. Distal end of metapodials with Chalicotherioid articular facets. The remainder of the foot fragments which constitute the type appear, however, to differ much from corresponding parts of the genera and species known of the family. This genus may well represent a totally different group of primitive ungulates doubtfully related to the Chalicotheres. Eocene; France.

Eomoropus Osborn. Premolar crowns simple, premolar metaconid without metastylids, large hypoconid on M_3, fibula greatly reduced. Upper Eocene; Washakie Basin, Wyoming.

Phyllotillon Pilgrim. Inner cusp of upper premolars united to ectoloph by double instead of single crest, molars long. (?) Oligocene. Nari beds, Bugti Hills.

Subfamily 2. Moropodinae.

Distal face of astragalus articulating with navicular only; fore and hind limbs of subequal length; trapezium present; Mc. V. present in some forms (Moropus).

Fig. 221.

Moropus elatus Marsh. Lower Miocene, Nebraska. Palatal aspect of skull lacking premaxillæ. 1/5. (After Holland and Peterson.)

Reproduced by permission from The Memoirs of the Carnegie Museum.

Moropus Marsh (Figs. 221, 222). Dentition $\frac{?\,0.3.3.}{3.0.3.3.}$. Upper molars longer than broad, external face of ectoloph relatively vertical, skull long and narrow; fore feet functionally tridactyl, trapezium present; Mc. III. longest; dorsal surface of metacarpal shafts straight longitudinally. Distal face of astragalus articulating with navicular only; Mt. III. and IV. of subequal length, fibula sometimes articulating with calcaneum, third trochanter of femur well developed; fore and hind limbs of subequal length. Lower and (?) Middle Miocene; Western North America.

Nestoritherium Kaup (*Ancylotherium* Gaudry) (Fig. 223). Dentition $\frac{?\,?\,3.3.}{?\,?\,3.3.}$. M^2 and M^3 longer than broad; skull long and narrow; carpus relatively low, trapezium present (?), manus and pes tridactyl, shafts of metacarpals

curved; astragalus articulating with navicular only; Mt. III. the longest in the pes. Lower Pliocene; Pikermi and Veles, Greece; Samos.

Fig. 222.

Moropus elatus Marsh. Lower Miocene, Nebraska. Right hind-foot, outer (*a*) and anterior (*b*) views. 1/8. (After Holland and Peterson.)
Reproduced by permission from The Memoirs of the Carnegie Museum.

Fig. 223.

Nestoritherium (*Ancylotherium*) *pentelici* Gaudry. Lower Pliocene, Pikermi, near Athens. Right radius, ulna, and base of fore-foot. 1/12. (After Gaudry.)

Subfamily 3. Macrotheriinae.

Distal face of astragalus articulating with navicular and cuboid as in other Perissodactyla; fore limbs longer than hind limbs; trapezium and Mc. V. wanting.

Macrotherium Lartet (*Anisodon* Lartet) (Fig. 224). Dentition $\frac{? ? 3.3.}{3.1.3.3.}$. Length and breadth of superior molars subequal, ectoloph extended inwards; humerus slender, radius and ulna long; Mc. IV. and Mt. IV. longest in manus and pes; astragalus low, broad, and articulating with both the navicular and the cuboid; pes short. Miocene; France and Germany.

Chalicotherium Kaup (Fig. 225). Dentition $\frac{? ? 3.3.}{? ? 3.3.}$. Upper molars broader than long, ectoloph extended inwards; dentition relatively short; proximal phalanx shorter than in *Macrotherium*. Miocene and Pliocene; Europe and India. Probably also in Pleistocene of Uganda (C. W. Andrews, Nature, vol. 112, 1923, p. 696).

Circotherium Holland and Peterson. Dentition $\frac{0.0.3.3.}{0.1.3.3.}$. M^1 broader than long. M^2 and M^3 breadth and length subequal; premaxilla short

and delicate; mandible reduced in length anteriorly but symphysis heavy; short muzzle; brachycephalic. This genus is founded on the front of skull

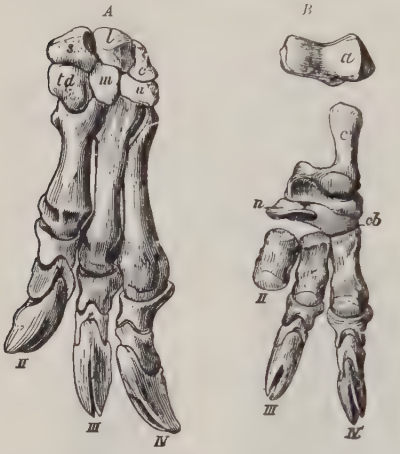


Fig. 224.

Macrotherium giganteum Gervais. Middle Miocene, Sansan (Gers), France. *A*, Left fore-foot. *B*, Left hind-foot, with separate upper view of astragalus (*a*). 1/8. (After Gervais.)

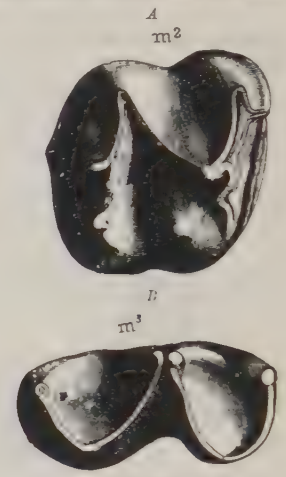


Fig. 225.

Chalicotherium goldfussi Kaup. Lower Pliocene, Eppelsheim, Hesse-Darmstadt. *A*, Second upper molar. *B*, Last lower molar. 2/3.

and lower jaw of *Chalicotherium* (*Anoplotherium*) *siralense* Falc. and Caut., from the Pliocene of the Siwalik Hills, India.

The following is of uncertain position: *Chalicotherium bilobatum* Cope. Oligocene; Swift Current River, Canada.

Suborder D. ARTIODACTYLA Owen. (Paraxonia Marsh.)

Even-toed Ungulates.[1]

Unguligrade or digitigrade ungulates with an even number of digits, the two middle of which are equally developed and much stouter than the lateral ones, which are often much reduced or aborted. Astragalus with ginglymoid trochleae proximally and distally. Carpal and tarsal bones alternating. Dentition complete, or incisors and canines absent, especially in the upper jaw. Cheek teeth bunodont, bunoselenodont, or selenodont. Femur without third trochanter. Fibula articulating with the calcaneum.

In contrast to the decadent perissodactyls, the artiodactyls constitute an existing group the most abundant in forms, the most dominant, and the most widely distributed of all the ungulates. They culminate in the bunodont suillines and the selenodont ruminants, which differ strikingly

[1] *Cope, E. D.*, The Artiodactyla. Amer. Naturalist, vol. xxii., 1888; vol. xxiii., 1889.—*Kowalevsky, W.*, Palaeontographica, vol. xxii., 1873-74.—*Sinclair, W. J.*, Bunodont Artiodactyla of Lower and Middle Eocene of North America. Bull. Amer. Mus. Nat. Hist., 1914.—*Stehlin, H. G.*, Säugetiere des Schweizer. Eocäns. Abh. Schweiz. palaont. Ges., vol. xxiii., 1906; xxv., 1908; xxvii., 1910.

from each other, but which through numerous extinct intermediate forms are brought into closest relations. The distinguishing character of the artiodactyls is the even number of digits. The middle digits (III and IV) are always equally developed, the lateral toes are more slender or quite rudimentary, the first digit or pollex usually occurring only in some few extinct forms (*Agriochoeridae*, *Anthracotheriidae*). The weight of the body is borne by the two median digits, the axis of the extremities falling between these.

The artiodactyls embrace in part slender, long-limbed, in part clumsy, short-limbed forms. In the more primitive types the skull recalls that of the carnivores and perissodactyls, but in the specialised forms, through the lengthening of the facial bones, the development of air-cells in the frontal region, of horn-cores, horns, etc., the skull acquires a very distinctive character. The lachrymals appear to be fairly expanded on the upper surface of the skull, and in the ruminants frequently exhibit rather deep depressions (lachrymal fossae) for the reception of sebaceous glands. The frontals always enter into the formation of the brain-case, and sometimes attain very large size. The mandible is usually long, slender, and low, with an ascending coronoid process.

The dentition is originally composed of forty-four teeth, which in the more primitive forms are arranged in a continuous series. Through the lengthening of the jaw or the suppression of the anterior premolars, and sometimes of the upper canines also, diastemata arise between the front teeth and the cheek teeth; these are longest in the ruminants, where the lower canine lies close to the incisors and assumes the form and functions of a cutting tooth (except in *Myotragus* where the lower front teeth are reduced to a single enlarged pair of incisors). The reduction, modification, or suppression of the incisor and canine teeth begins in the upper jaw earlier than in the mandible. Vestiges of superior incisors are still to be recognised in the embryo of the sheep.

In all older and more primitive forms, the cheek teeth are brachyodont; in the ruminants they are in part prismatic. The development of cement as a rule also accompanies this deepening of the teeth. The crown of the molars in the later forms is quadritubercular. The cusps are arranged in opposite pairs. Originally the superior molars were quinquetubercular, and the lower molars sexitubercular. But in the latter the paraconid and metaconid were soon lost or reduced, or the paraconid fused with the metaconid, while in the superior molars the anterior intermediate cusp or protoconule was soon united with the protocone. The second inner cusp of the upper molars is not the real hypocone, but the metaconule. In *Caenotherium* and *Dichobune* the posterior half of the upper molars shows three cusps, the innermost of which is, according to Stehlin, an accessory one.

Accessory pillars as well as strongly developed basal cingula occur in many artiodactyls. If the tubercles remain conical, the dentition is bunodont; if they assume a V-shaped or crescentic form, the dentition is bunoselenodont or selenodont. In selenodont upper molars, the crescents of the external cusps open outward and generally meet, forming at the point of union an ectoloph with a vertical fold (mesostyle).

The internal cusps may remain either conical or V-shaped, or the crescents

may inclose curved pits. The inferior molars are distinguished from those above by their narrower breadth. In the bunodont forms the four cones remain conical and generally distinct; in selenodont types the external cones are V-shaped or crescentic and the opening is directed inward. Their usually compressed internal cusps as a rule meet, thus forming an internal serrated crest. The posterior lower molar nearly always exhibits a fifth unpaired cone or crescent, while the posterior upper molar is frequently somewhat larger and never smaller than the preceding molars. Complete agreement between molars and premolars never occurs in the *Artiodactyla*, even though in individual forms of the most modern types (*Dicotyles*) and in the terminal members of some extinct series (*Dichodon*, *Agriochoerus*) this condition appears to be approximated. The artiodactyl dentition is typically heterodont, and the structure of the premolars is considerably less complex than that of the molars. Sometimes the last premolar has the appearance of a molar; much more often, however, it is similar to half a molar.

The milk dentition contains in concentrated essence the elements of the permanent dentition. Incisors and canines deviate only slightly from their successors; on the other hand, the milk cheek teeth present greater diversity than in the perissodactyls. The posterior upper milk tooth has the form and structure of a true molar. The last inferior milk tooth closely resembles the third molar, yet does not consist of the typical four cusps or crescents and a talonid, but the third pair of cusps or crescents is here on the anterior end of the tooth. In general, however, the anterior milk teeth bear more resemblance to the premolars than to the molars.

The scapula is narrow and triangular in form. The clavicle is absent except in the more primitive families. The humerus is in the more specialised forms shorter than the forearm, and longer only in some of the more primitive. The radius and ulna either remain distinct or the distal portion of the latter, sometimes also the proximal, is completely fused with the radius. The carpus contains the same elements as seen in the perissodactyls and shows the same lateral displacement of the distal series; hence the magnum and unciform always support two ossicles of the proximal row. In more specialised selenodonts the fusion of the magnum and trapezoid, and often the complete atrophy of the trapezium, occur.

Five metacarpals are thus far known only in *Agriochoeridae* and *Anthracotheriidae* (Fig. 226, *A*). The first metacarpal, however, is here very small, vestigial, and only in some *Agriochoeridae* carries short phalanges. In all the most primitive forms as well as in all existing *Suidae* and *Hippopotamidae*, the four remaining metacarpals are distinct. In the ruminants, the lateral metacarpals are much reduced, and their respective digits either hang free as short terminal claws or are completely atrophied. If the lateral metapodials become styloid or entirely disappear, the median ones generally show a tendency to coalesce. The "cannon bone" thus formed always has, however, two medullary cavities, the distal end remains cleft and exhibits two articular surfaces. The point of union is indicated externally by a furrow on the anterior side of the cannon bone. Mobility and speed depend entirely on the length of the metapodials. In the fleet-footed ruminants, therefore, these are long and slender, but in the clumsy hippopotamus, pig and their allies, they are short and compact. The

two equally developed metacarpals (III. and IV.) always exceed the two lateral ones (II. and V.) in length and strength, and this difference increases as the extremities become fitted for swift running and leaping. In the more specialised forms with four or two digits, sharp median ridges or keels are developed on the distal articular surface of the anterior and posterior metapodials.

In the primitive artiodactyl fore-foot, the first metacarpal articulates with the trapezium, the second with the trapezium, trapezoid and magnum, the third with the magnum and unciform, and the fourth and fifth with the unciform. This arrangement may be modified by the reduction of the lateral digits (Fig. 226, *A*, *B*); in this kind of modification, which has been

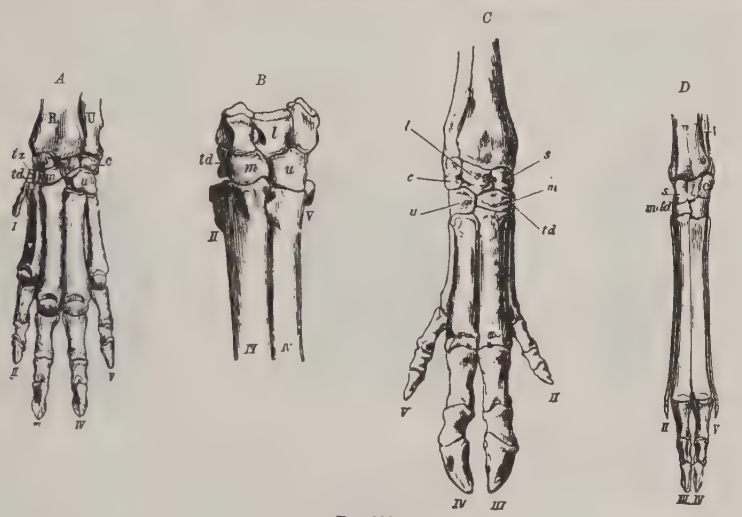


Fig. 226.

Fore-foot of *A*, *Oreodon*; *B*, *Xiphodon* (with inadaptive reduction); *C*, *Sus*; and *D*, *Tragulus* (with adaptive reduction).

defined by Kowalevsky as "inadaptive reduction," each metapodial inflexibly maintains its place among the carpals pertaining to it; hence the second metacarpal articulates with the magnum, trapezoid and trapezium. In "adaptive reduction" (Fig. 226, *C*, *D*) the two median metacarpals continue subequal in height, their proximal articular surfaces broaden out, push the lateral metapodials outward and backward, and thus extend their contact with the carpus. In this arrangement, the second metacarpal is excluded from the magnum, and articulates with but part of the trapezoid and with the trapezium. According to Kowalevsky, this modification affords greater strength to the foot, and qualifies its owner for a more successful struggle for existence. In fact, all existing artiodactyls with reduced extremities belong to the "adaptive" series.

The pelvis is elongated and the ilium narrow. The femur lacks the third trochanter. In more primitive forms the tibia and fibula are distinct and well developed; in more specialised types the fibula becomes reduced to a splint-like proximal vestige, and a separate distal vestige which articulates

with the calcaneum. On its anterior side, above, the calcaneum (Fig. 227) has a rounded facet (*p*) for the fibula. In the astragalus (Fig. 228) the superior and anterior articular surfaces (trochlea) for the tibia are deeply excavated (*t*); the distal portion (*n*, *cub*) resting on the navicular and cuboid is not truncate as in the perissodactyls, but likewise forms a convex articular face, which passes into a large rounded facet (*cal*) on the posterior side. In more primitive tetradactyl forms with well-developed lateral digits, the tarsal elements remain distinct. In the ruminants, as a rule, a fusion of the cuboid and navicular takes place, the second and third cuneiforms likewise coalesce, and sometimes even the cuboid, navicular and two cuneiforms unite into a single bone.

In the pes as in the manus there is a gradual reduction or atrophy of the lateral metapodials and digits. The first metatarsal is always vestigial, this remnant usually representing the phalanges also. Through the partial atrophy of one lateral digit, the hind-foot becomes tridactyl in the *Anoplotheriidae* and *Dicotyles*. The two median metatarsals fuse into a

Fig. 227.

Calcaneum of *Anoplotherium commune* Cuvier, anterior aspect. *as*, Articular facet for astragalus; *cub*, for cuboid; *p*, for fibula. (After Gaudry.)

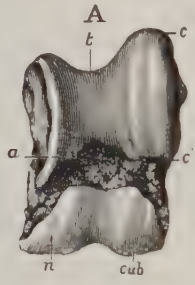


Fig. 228.

Astragalus of *Helladotherium duvernoyi* Gaudry. *A*, Anterior aspect; *B*, posterior aspect; *a*, free inner border; *c*, *c'*, lateral facet for calcaneum; *cal*, posterior facet for calcaneum; *cub*, facet for cuboid; *n*, facet for navicular; *t*, trochlea for tibia. (After Gaudry.)

cannon bone, this coalescence sometimes occurring in the pes even though the metapodials of the manus still remain distinct (*Hyaemoschus*, *Dicotyles*). In general, reduction and co-ossification appear earlier and show more distinctly in the pes than in the manus. In the "inadaptive" development of the extremities, the metatarsals maintain their position among the corresponding tarsal elements. In the "adaptive" reduction the proximal ends of the principal metatarsals expand and push the lateral metapodials outward and backward. The digits of both extremities are similar in structure. The terminal phalanges are triangular, encased in hoofs, and only in the *Anoplotheriidae* and *Agriochoerus* are clawlike.

For a phylogenetic understanding of the modification of the extremities in the artiodactyls, it is interesting to note that in the more specialised forms (*Cavicornia*) the co-ossified bones of the adult condition are separately developed in the embryo, and thus correspond to the forms geologically older. The developmental stages that apparently so widely separate the clumsy short tetradactyl foot of *Hippopotamus* and the slender elongated double-hoofed extremities of the ruminants, are brought into closest connection through numerous intermediate fossil forms, and therefore up to a certain

point also become accelerated in the ontogeny of the highest forms of the even-toed ungulates.

Taking the dentition as a basis, the *Artiodactyla* fall into three principal tribes: *Bunodontia*, *Bunoselenodontia* and *Selenodontia*. Through transitional forms (such as *Dichobunidae*), however, these are related to each other, and may be separated into fifteen families, as follows:

1. *Bunodontia.*	2. *Bunoselenodontia.*	3. *Selenodontia.*
1. *Suidae.*	1. *Anthracotheriidae.*	1. *Xiphodontidae.*
2. *Leptochoeridae.*	2. *Anoplotheriidae.*	2. *Caenotheriidae.*
3. *Hippopotamidae.*	3. *Dichobunidae.*	3. *Agriochoeridae.*
		4. *Camelidae.*
		5. *Tragulidae.*
		6. *Hypertragulidae.*
		7. *Cervicornia.*
		8. *Antilocapridae.*
		9. *Cavicornia.*

Tribe 1. BUNODONTIA.

Family 1. Suidae Gray. Swine.[1]

Dentition complete, brachyodont and bunodont. Dental formula: $\frac{3\text{-}2.1.4\text{-}3.3.}{3.\ 1.4\text{-}3.3.}$. *Superior and inferior molars with four obtuse conical low tubercles and frequently numerous wartlike accessory conules. In the oldest genera a fifth tubercle (protoconule) present, or premolars less complex than molars. Canines very strongly protuberant. Carpals and tarsals not coalesced. Posterior half of astragalus shifted somewhat laterally toward the superior portion. Feet tetradactyl, rarely two-toed. Metapodials generally quite distinct. Lateral digits more slender and shorter than median ones.*

The *Suidae* are very closely allied to the *Anthracotheriidae*, at least in their oldest types, and may have arisen from the same stem. Their living representatives are now indigenous in Europe, Asia, Africa and America. Fossil *Suidae* first appear in the Eocene of Europe, yet the greatest development of this family occurs in the Miocene, Pliocene, Pleistocene and Recent. In the New World they are less abundantly developed.

FIG. 229.

Cebochoerus minor Gervais. *A*, Upper fourth premolar and molars. Bohnerz, Egerkingen. 1/1. (After Rütimeyer.) *B*, Lower cheek teeth. Phosphorites, Quercy. 1/1. (After Gaudry.)

Eohyus Marsh. A doubtful form, imperfectly known. Eocene; Wyoming.

Cebochoerus Gervais (Figs. 229, 230). Upper canines vertical, dagger-like, lower canine developed as fourth incisor, and first premolar as canine. First

[1] *Peterson, O. A.*, Memoirs of the Carnegie Museum, vol. ii., 1905; vol. iv., 1909.—*Scott, W. B.*, The Osteology of Elotherium. Trans. Amer. Phil. Soc., 1898, p. 273.—*Stehlin, H. G.*, Geschichte des Suidengebisses. Abh. Schweiz. Pal. Ges., 1899, 1900.

molar without basal cingulum; superior molars nearly quadrate, quinquetubercular, with three cusps in the anterior half. Lower jaw very deep behind, with rounded angular process. Last inferior molar with talonid. Middle Eocene; Egerkingen. Upper Eocene; Mauremont. *C. helveticus* Pict. Phosphorites of Quercy and St. Hippolyte de Caton. *C. minor* Gerv.

Acotherulum Gervais. Superior molars quadrate,

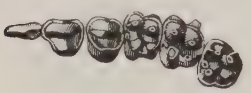


Fig. 230.

Cebochoerus ruetimeyeri Stehlin. Middle Eocene Bohnerz, Egerkingen. Upper cheek teeth, 1/1. (After Stehlin.)

Fig. 231.

Achaenodon robustus Osborn. Middle Eocene (Bridger beds), Washakie, Wyoming. Skull and lower jaw. 1/6. (After Osborn.)

all cusps close together with small fifth tubercle. Upper Eocene; Débruge, and the older Phosphorites, Quercy.

Choeromorus Pictet (*Leptacotherulum* Filhol). Superior molars quinquetubercular, broader than long. Posterior part of lower jaw with sinuated lower margin. Ancestors of the typical *Suidae*. Canines and first lower premolars normal. Upper Eocene; Mauremont. *C. helveticus* Pictet.

Choeropotamus Cuvier. Molars usually

Fig. 232.

Elotherium crassum Marsh. Oligocene (White River beds), Dakota. Skull, lateral aspect (*A*), and upper aspect (*B*). 1/8. (After Marsh.)

with four angular main cusps and two or three small intermediate conules. Premolars short, simple. First upper *P* enlarged, first lower *P* as canine. Lower canine developed as incisor. Superior canine long, dagger-shaped.

Lower jaw low behind, elongated. Upper Eocene; France and England. *C. parisiensis* Blainville.

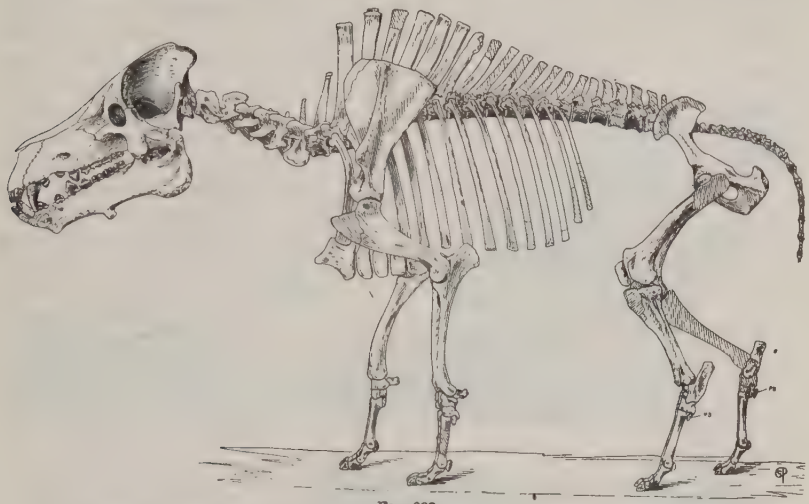


FIG. 233.

Dinohyus hollandi Peterson. Lower Miocene, Nebraska. Restored skeleton. 1/26. (After Peterson.)
Reproduced by permission from The Memoirs of the Carnegie Museum.

Achaenodon Cope (? *Parahyus* Marsh) (Fig. 231). Skull bear-like. Incisors and canines of the full number, conical. Molars quadritubercular; premolars trenchant, monocuspid. Eocene; Bridger and Uinta formations, Wyoming. *A. insolens* Cope. *A. robustus* Osborn.

Protelotherium Osborn. Three superior premolars, superior molars quinquetubercular. Zygomatic arch without process. Frontal broad. Tetradactyl. Upper Eocene; Uinta beds. *P. uintense* Osborn.

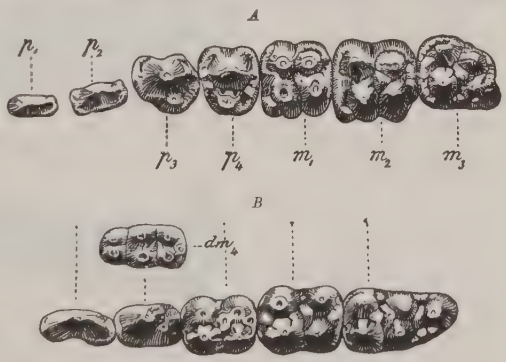


FIG. 234.

Palaeochoerus meisneri Meyer. Lower Miocene, Ulm, Württemberg. *A*, Upper, and *B*, lower, cheek teeth. 1/1.

Elotherium Pomel (*Entelodon* Aymard; *Archaeotherium* Leidy) (Fig. 232). Superior molar quinquetubercular, three cusps being in the anterior half of the tooth. All molars with strong basal cingulum. Last inferior molar without talonid. Zygomatic arch very well developed, with descending process. Mandible also with protuberances on anterior part of lower border. Extremities always with two digits. American species show fourteen dorsal and six lumbar vertebrae. The osteological details harmonise on the

whole more with the *Anthracotheriidae* than with the *Suidae*. Oligocene; Ronzon and Lobsann (Alsace), and Quercy Phosphorites. Also White River Oligocene, John Day beds and Lower Miocene of North America.

Dinohyus Peterson (Fig. 233). Proportionally short alveolar border of premaxilla with incisors more crowded, the median one reduced; chin short, p 3 nearly square in outline, p 4 with large deuterocone, lower molars with subequal height of posterior and anterior tubercles which are separated by narrow cross valleys. Trapezium absent, fibula co-ossified with the tibia. Miocene; Nebraska.

Fig. 235.

Palaeochoerus waterhousi Pomel. Lower Miocene, St. Gerand-le-Puy, Allier. *A*, Skull and lower jaw, lateral aspect. 1/3. *B*, *C*, Upper and lower teeth. 1/2. (After Filhol.)

Palaeochoerus Pomel (Figs. 234, 235). Teeth in nearly continuous series. Canines not much stronger developed than incisors and premolars. Superior and inferior molars quadritubercular, with basal cingulum. Last inferior molar with talonid. Lower Miocene; Europe. *P. meisneri* Meyer. *P. typus* Pomel. Middle Miocene. *P. aurelianensis* Stehlin.

Propalaeochoerus Stehlin. Oligocene Phosphorites; Quercy.

Choerotherium Depéret (*Colobus* Fraas). Cheek teeth small and very simple. Upper Miocene; Sansan, Steinheim, etc.

Xenochoerus Zdarsky. Premolar very complicated, molar-like. Upper Miocene; Styria.

Hyotherium Meyer (Fig. 236). Like *Palaeochoerus*, but larger. Premolars more strongly compressed and elongate, and fourth premolar in both jaws complicated. Superior canines with divided root. Cusps of molars angular. Middle and Upper Miocene; Europe. *H. soemmeringi* Meyer. Pliocene? Siwalik, India. *H. perimense* Lydekker.

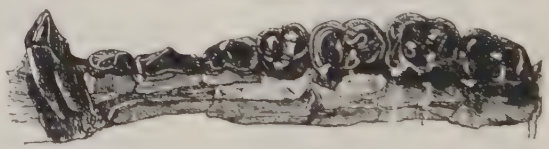


Fig. 236.

Hyotherium soemmeringi Meyer. Upper Miocene, Eibiswald, Steiermark. Upper jaw. 1/2. (After Peters.)

Perchoerus Leidy. Oligocene; White River beds. *Chaenohyus* and *Bothrolabis* Cope. *Desmathyus* Matthew. Lower Miocene. *Thinohyus* Marsh. Upper Miocene of North America. These are Palaeochoeroid predecessors of *Dicotyles*.

Dicotyles Cuvier. Dental formula: $\frac{2.1.3.3.}{3.1.3.3.}$ Superior canines triangular, vertical. Premolars and molars with two pairs of main cusps and small accessory conules. Diastema long. Ulna united with radius. The two median tarsals partially coalesced. Metatarsals III. and IV. proximally fused. Metatarsal V. reduced. Recent and Pleistocene; North and South America.

Platygonus Le Conte. Only three premolars, with long diastema preceding them. Premolars bicuspid. Cusps of molars joined to crests. Upper Miocene, Pliocene and Pleistocene; North America.

Prosthennops Matthew and Gidley. Superior dentition: 2.1.3.3. Diastema moderate. Upper Miocene (Loup Fork beds); Dakota.

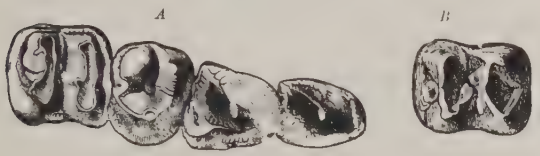


FIG. 237.

Listriodon splendens Meyer. Miocene (Sarmatian), Nussdorf, Vienna. *A* Premolars and first molar of upper jaw. *B*, Second lower molar. 3/4.

FIG. 238.

Sus erymanthius Roth and Wagner. Lower Pliocene, Pikermi, Athens. Upper cheek teeth. 1/2. (After Gaudry.)

FIG. 239.

Sus scrofa Linn. Tarsus and base of metatarsus. 1/2. (After Flower.)

Doliochoerus Filhol. Cusps with crest-like arrangement. Oligocene; Phosphorites.

Listriodon Meyer (Fig. 237). Dental formula: $\frac{3.1.3.3.}{3.1.3.3}$ Superior incisors broad, triangular, and bent upward; inferior, directed obliquely forward. Superior canines very thick, short, triangular, bow-shaped, curved upward; lower canines long, triangular, strongly curved, with worn posterior surfaces. Molars with two transverse crests, superior premolars trigonodont. Middle and Upper Miocene; Europe. *L. splendens* Meyer. Also Siwalik beds; India.

Hippohyus Falconer. Tubercles with numerous folds of enamel. Siwalik, India.

Sus Linn. (Figs. 238, 239). Incisors and canines as in *Listriodon*, molars with four blunt main cusps and numerous wart-like accessory tubercles. Third superior molar with long talon. Now living in Europe, Asia, and

northern Africa. Fossil in the Upper Miocene; Monte Bamboli. *S. choeroides* Pomel. Lower Pliocene; Eppelsheim, Pikermi, etc. *S. antiquus* Kaup. *S. erymanthius* Roth and Wagner. Also China and India. Upper Pliocene; Europe. *S. strozzi* Meneghini. Pleistocene; Europe. *S. scrofa* Linn.

Of the foregoing genera, *Elotherium*, *Dinohyus*, *Achaenodon*, and one or two related forms, may perhaps be recognised as constituting a distinct family, *Elotheriidae*, differing from *Suidae* in the more primitive structure of incisors, canines and premolars.

Family 2. **Leptochoeridae** Leidy.

Superior molars much shorter than broad, tritubercular; inferior molars quadritubercular, their anterior half being higher than the posterior half. Lateral metapodials very slender.

Leptochoerus Leidy (*Laopithecus* Marsh; *Stibarus*, *Menotherium* Cope). Oligocene; White River beds, Dakota.

Family 3. **Hippopotamidae** Gray.[1]

Large, heavy amphibious ungulates, with complete bunodont dentition. Dental formula: $\frac{3\text{-}2.1.4.3.}{3\text{-}1.1.4.3.}$ *Superior and inferior cheek teeth with four blunt lobed cusps,*

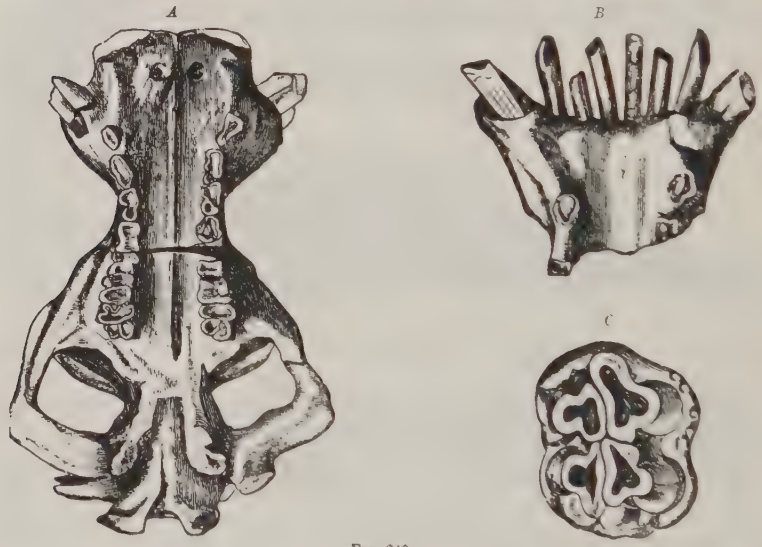


Fig. 240.

Hippopotamus (*Hexaprotodon*) *sivalensis* Falconer and Cautley. Pliocene, Siwalik Hills, India. *A*, Palatal aspect of skull, 1/8. *B*, Symphysis of lower jaw from above, 1/8. *C*, Third upper molar, 1/2. (After Falconer.)

which when worn present a trefoil-like upper surface. Premolars much simpler than molars. Superior canines very stout, short, with anterior wear; inferior canines

[1] *Major, C. I. Forsyth*, Hippopotamus madagascariensis. Geol. Mag., 1902, p. 193.—Pigmy Hippopotamus from Cyprus. Proc. Zool. Soc., 1902, p. 107. *Reynolds, S. H.*, Pleistocene Hippopotamus. Mon. Palaeont. Soc., 1920 (1922). *Stromer, E. von*, Wirbeltierreste aus dem Mittelpliocän des Natrontales, Ägypten. Zeitschr. Deutsch. Geol. Gesell., 1914.

exceedingly large, strongly curved, triangular, with edges sharpened through wear of posterior surface. Inferior incisors cylindrical, very long, rootless, directed forward. Carpals, tarsals and metapodials distinct. Feet tetradactyl, the lateral digits but little more slender and shorter than the medians. Terminal phalanges with nail-like hoofs.

The single existing genus of this family is confined to tropical Africa. Fossil representatives are found in the Pliocene and Pleistocene of Asia, Africa, and Europe.

The genus *Hippopotamus* Linn. (Fig. 240) is divided into two subgenera, *Hexaprotodon* and *Tetraprotodon* Falconer, these being based on the number of incisor teeth present. Lower Pliocene; India. *H. sivalensis* Falconer and Cautley. One species, also, in the Pliocene of Algiers and Egypt. *H. hipponensis* Gaudry. In the Pliocene of Val d'Arno. *H. major* and *H. pentlandi* Falconer, which also occur in the Lower Pleistocene of Europe, both being closely allied to the existing *H. amphibius* Linn. In the Pleistocene of Algiers are several species; also in the late Pleistocene of Madagascar is a small very abundant form, *H. madagascariensis* Grandidier. One small species also from Malta, Crete and Cyprus. *H. minutus* Blainv. In the Pleistocene of Java is found *H. sivajavanicus* Dubois.

Tribe 2. BUNOSELENODONTIA.

Family 4. Anthracotheriidae Leidy.[1]

Extinct artiodactyls with complete dentition. Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. *Superior molars with four main cusps and one intermediate tubercle in the anterior half of the tooth; inferior molars with crescentic external cusps, conical on the inside. Premolars short, the three anterior ones monocuspid, usually separated from the canine by a diastema; only the last premolar with a secondary cusp. Carpals, tarsals and metapodials not co-ossified. Feet tetradactyl, the lateral digits more slender and shorter than the median ones.*

The *Anthracotheriidae* form a primitive group of artiodactyls which were especially abundant in Europe, but were more sparingly distributed in North America, northern Africa and India. The oldest remains are found in the Upper Eocene Bohnerz and Phosphorites, the chief deposits for *Anthracotherium* being the Oligocene. The latest forms became extinct in the Miocene.

Anthracotherium Cuvier (*Heptacodon, Octacodon* Marsh) (Fig. 241). Superior molars broader than long, with four V-shaped or conical cusps and an anterior crescentic intermediate cone. Inferior molars quadritubercular, the last tooth with a strong talonid. Incisors above and below spatulate, tapering. Canine very powerfully developed. Diastema small. Abundant in the Oligocene of Europe, especially in coal-bearing deposits. The species vary in size between

[1] *Cooper, C. Forster*, Palaeont. Indica, n.s., vol. viii., no. 2, 1924.—*Filhol, H.*, Mammifères fossiles de Ronzon. Ann. Soc. Géol., 1882, p. 85.—*Kowalevsky, W.*, On the Osteology of the Hyopotamidae. Philos. Trans. 1873.—Anthracotherium. Palaeontographica, 1873, vol. xxii.—*Scott, W. B.*, Structure and Relationship of Ancodus. Journ. Acad. Nat. Sci. Philad. 1895.—*Schmidt, M.*, Paarhufer der fluviomarinen Schichten des Fajum. Geol. u. Palaeont. Abhandl., 1913.—*Stehlin, H. G.*, Revision der europäischen Anthracotherien. Verhandl. naturf. Ges. Basel, 1910.

the rhinoceros (*A. magnum* Cuvier) and the pig (*A. minus* Cuvier, *A. valdense* Kowalevsky). In the Upper Oligocene (Protoceras beds) of Dakota similar forms also occur, named *Heptacodon*, *Octacodon* Marsh.

Brachyodus Gervais. Dental series continuous. Upper molars quadrate. Oligocene of Europe, *B. porcinus* Gerv. Middle Miocene of Europe, *B. onoideus* Gerv. In Egypt, *B. africanus* Andrews. Also Lower Miocene of British East Africa and India.

Ancodus Pomel (*Hyopotamus* Owen *non* Rütimeyer; *Bothriodon* Aymard) (Fig. 242). Large-sized, the skull longer and lower than in *Anthracotherium*. Canines weaker, and the first premolar separated from adjacent teeth by a wide interval. Cusps of the molars above and below distinctly V-shaped. Inner cusps of the lower molars pointed. Oligocene; especially abundant at Ronzon, Haute Loire. *A. velaunus* Cuvier sp., *A. bovinus* Owen sp. In the Oligocene of Egypt, *A. gorringei* Andrews. Oligocene; North America. *A. americanus* Leidy, *rostratus* Scott, *brachyrhynchus* O. and E., *leptodus* Matthew, from successive horizons of the Oligocene in South Dakota. The later North American species are characterised by more quadrate and narrower superior molars and shorter muzzle. In *A. rostratus* Scott there is a large complete pollex.

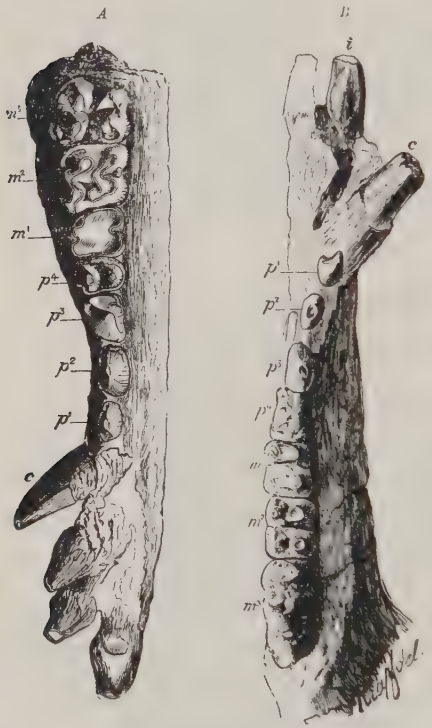


FIG. 241.

Anthracotherium magnum Cuvier. Oligocene, La Rochette, near Lausanne. *A*, Upper jaw. *B*, Lower jaw. $\frac{1}{3}$.

Merycopotamus Falconer and Cautley. Superior molars with but four V-shaped tubercles. Lower Siwalik beds, India. *M. nanus* Lydekker. Also in Tunis.

Rhagatherium Pictet (*Hyopotamus* Rütimeyer). Superior molars with five pointed cusps and mesostyle. Superior last premolar molariform, the other premolars very much complicated and, with exception of the first, elongated. A diastema in front of P_2. • *R. valdense* Pictet. *R. frohnstettense* Kow.

Tapirulus Gervais. Tubercles of the molars strongly compressed laterally, and internally joined to a crest. Upper Eocene and Oligocene Bohnerz and Phosphorites.

Mixtotherium Filhol (*Adrotherium* Filhol; *Hyopotamus* Rütimeyer). Superior molars similar to those of *Ancodus* with strong mesostyle, subtriangular. Cusps V-shaped with exception of the protocone. Inferior molars with elongated inner cusps. Premolars very complicated and elongated. Canine

normal. Skull short, with small cranium and massive jugal. Lower jaw deep, similar to that of *Hyrax*. Eocene Bohnerz, Egerkingen. *M. gresslyi* Rütimeyer. Phosphorites, *M. cuspidatum* Filhol.

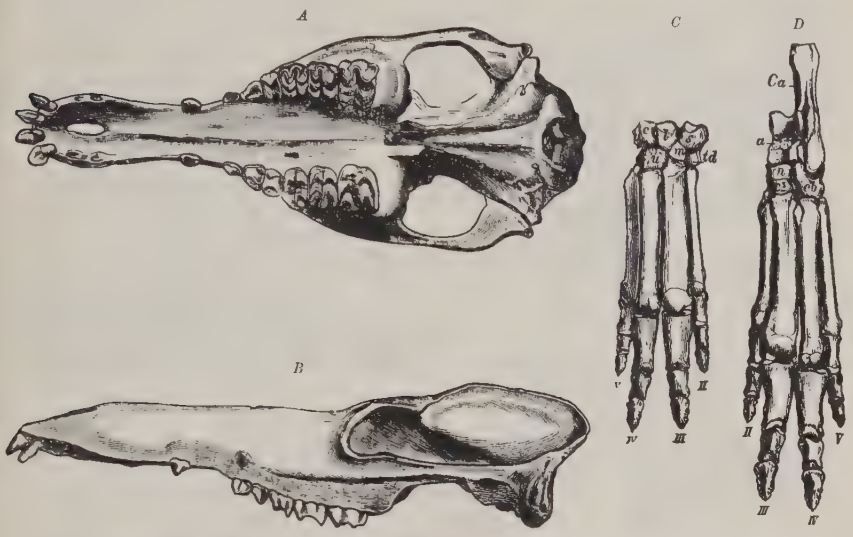


FIG. 242.

Ancodus (*Hyopotamus*) *velaunus* Cuvier sp. Oligocène, Ronzon, near Le Puy. Skull in palatal (*A*) and lateral (*B*) aspects. 1/4. (After Filhol.) Fore (*C*) and hind (*D*) foot. 1/5. (After Kowalevsky.)

Family 5. **Anoplotheriidae** Gray.

Dentition complete, either forming a continuous unbroken series or a small diastema between the anterior teeth. Dental formula : $\frac{3.1.4.3.}{3.1.4.3.}$. *Cheek teeth selenobunodont. Superior molars with four usually* V*-shaped main cusps and an intermediate tubercle between the anterior pair. External cusps of the lower molars crescentic, internal cusps conical, anterior double. Anterior premolars above and below much elongated and trenchant. Incisors, canines and premolars sometimes enlarged and trenchant. Carpals, tarsals and metapodials distinct. Feet with four, three or two digits, the two lateral toes shorter than the median ones and usually standing out at an angle. Terminal phalanges pointed, claw-like. Reduction of lateral digits inadaptive.*

All representatives of this family are extinct and are found in the Eocene and Oligocene of Europe.

The skull never bears bony processes and somewhat resembles that of *Camelus*, but the muzzle is shorter. The dentition exhibits various primitive characters ; and a coalescence of the carpal, tarsal or metapodial bones likewise never takes place. The pollex and fifth digit, as well as the hallux, are sometimes present as vestigial metapodials. In external habit the *Anoplotheriidae* more resemble the carnivores than the ungulates, especially by the long tail and the claw-like terminal phalanges.

Anoplotherium Cuvier (*Eurytherium* Gervais) (Figs. 243-245, 247, *A*). Ectoloph of superior molars W-shaped, the anterior inner cusp conical, the posterior V-shaped, the intermediate cone small. Canines premolariform. Inferior molars with two V-shaped crescents and three internal cones, the posterior of which shuts off the posterior crescent. The Anoplotheres were short-limbed, thick-set ungulates, provided with an unusually long and powerful tail. They were about the size of the tapir, probably lived on swampy lowlands, and used the tail as a swimming organ. Their three digits were perhaps connected by a membranous web. Abundant in the Upper Eocene; Europe. *A. commune* Cuvier. *A.* (*Eurytherium*) *latipes* Gervais.

Fig. 243.

Anoplotherium commune Cuvier. Upper Eocene (Gypsum), Montmartre, Paris. Skull and lower jaw. $^1/_5$. (After Blainville.)

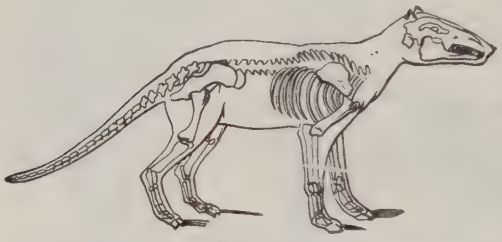


Fig. 244.

Anoplotherium commune Cuvier. Upper Eocene. Restoration by Cuvier.

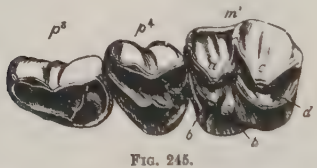


Fig. 245.

Anoplotherium latipes Gervais sp. Upper Eocene (Phosphorites), Escamps, Quercy. Third and fourth premolars and first molar of upper jaw. $^1/_1$.

Diplobune Rütimeyer (*Hyracodontherium* Filhol) (Figs. 246, 247, *B*, *C*). Very similar to *Anoplotherium*, but smaller and more delicate. The inferior molars are characterised by the fact that the two antero-internal cusps (α, β') are placed close to each other and form a bilobed pillar. The first superior incisor enlarged. Abundant in the Oligocene Bohnerz near Ulm and Pappenheim. *D. quercyi* Filhol. *D. bavaricum* Fraas. Quercy Phosphorites. *D. modicum* Filhol. Upper Eocene; Paris and Débruge. *D. secundarium* Cuvier.

Dacrytherium Filhol. Second and fifth digits complete. Phosphorites, Quercy.

Leptotheridium Stehlin and *Catodontherium* Depéret. Eocene Bohnerz of Switzerland.

Orthaspidotherium Lemoine. A small form from the Lower Eocene of Rheims. It probably belongs to this family.

Family 6. Dichobunidae.

Extinct artiodactyls with complete dentition $\frac{3.1.4.3.}{3.1.4.3.}$. *Superior molars (with*

the exception of the last) of most genera with three cusps in either half of the tooth, inner cusps V*-shaped, the others frequently conical. Inferior molars with conical inner cusps and* V*-shaped exterior cusps. Anterior inner cusps double. Anterior part of the inferior molars a little higher than the posterior. Premolars simple and elongated. Manus and pes tetradactyl. Lateral metapodials shorter and slender. Skull similar to that of Tragulus.*

This family differs from all artiodactyls in the presence of six cusps in

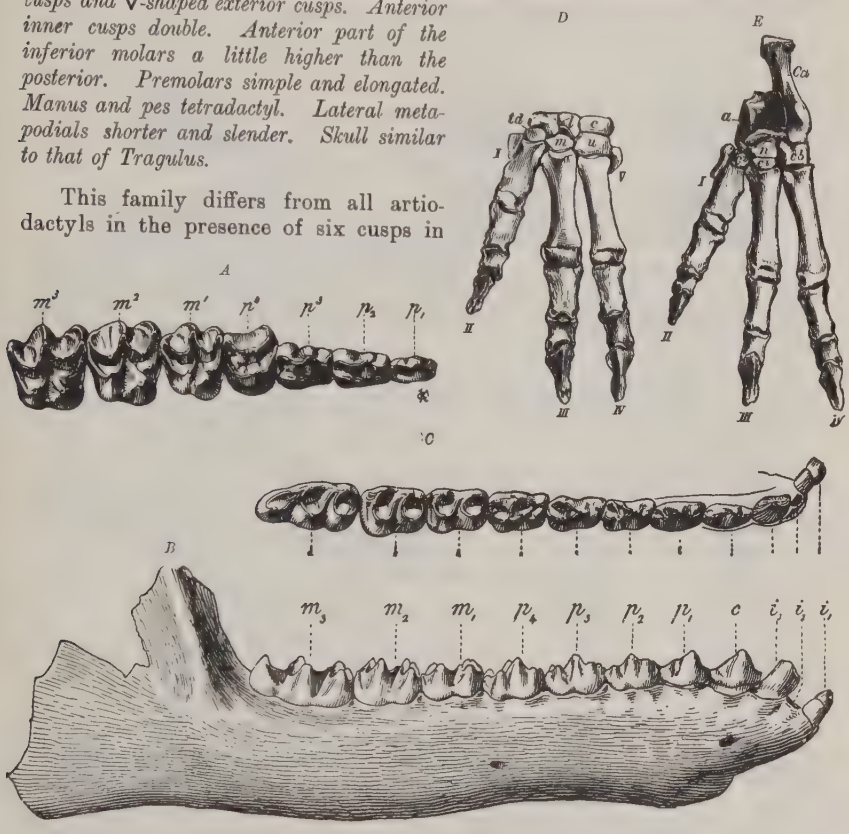


Fig. 246.

Diplobune quercyi Filhol. Oligocene (Bohnerz); Esselsberg, Ulm. *A*, Cheek teeth of upper jaw. *B*, *C*, Right ramus of lower jaw, and dentition from upper aspect. 2/3. *D*, Fore foot. *E*, Hind foot. 1/4.

the upper molars, notwithstanding the resemblance to the primitive *Suidae*, *Anthracotheriidae* and *Tragulidae*.

The *Dichobunidae* begin in Europe in the oldest Eocene and become extinct in the Middle Oligocene. In North America they are confined to the Eocene.

Dichobune (*Microchoerus* Wood, *Hyopotamus* Rütimeyer) (Fig. 248). Superior series of the teeth closed. Superior molars with mesostyle, all cusps nearly conical, premolars simple. Upper Eocene. *D. leporinum* Cuvier.

Mouillacitherium Filhol (*Necrolemur*, *Hyopsodus* Rütimeyer). Without protoconules in the superior molars. Eocene. *M. cartieri* Rütimeyer.

Meniscodon Rütimeyer (*Phenacodus*, *Protogonia* Rütimeyer). Of moderate size. Superior molars without mesostyle and with large parastyle. Middle Eocene; Egerkingen. *M. europaeus* Rütimeyer.

Metriotherium Filhol (*Deilotherium, Spaniotherium* Filhol). Large forms. Phosphorites of Quercy.

Protodichobune Stehlin. Lower Eocene of Epernay.

Homacodon Marsh. First and second superior molars sextubercular, third

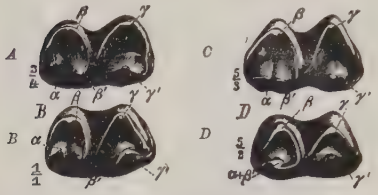


Fig. 247.

Lower molars of *A*, *Anoplotherium latipes* Gervais sp.; *B*, *Diplobune modicum* Filhol; *C*, *Diplobune minus* Filhol; and *D*, *Xiphodon* sp. Phosphorites, Quercy. (After Steinmann and Doederlein.)

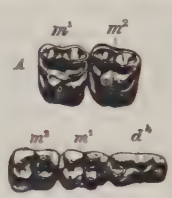


Fig. 248.

Dichobune leporinum Cuvier. Phosphorites, Escamps, Quercy. *A*, Two upper molars. *B*, Lower last milk-molar and two first molars. 1/1.

molar quinquetubercular, inferior molars quadritubercular, similar to those of *Dichobune* and *Helohyus* Marsh. Middle Eocene (Bridger beds); Wyoming.

Sarcolemur Cope. Inferior molars with much-pointed cusps. Middle Eocene (Bridger beds).

Diacodexis (*Trigonolestes*) Cope. Superior molars tritubercular. Lower Eocene (Wasatch beds); Wyoming. *D.* (*Pantolestes*) *brachystomus* Cope.

Tribe 3. SELENODONTIA.

Family 7. Xiphodontidae Flower.

Cheek teeth selenodont. Superior molars with five or four crescents, intermediate cone in anterior half. Inferior fourth premolar and superior fourth premolar often very complex, the other premolars elongated. Feet slender, long, with two digits; median metapodials and tarsalia distinct; lateral metapodials reduced to very small vestiges. Upper Eocene; Europe.

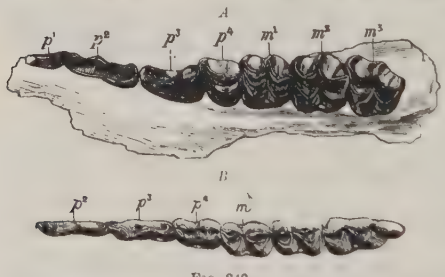


Fig. 249.

Xiphodon gracile Cuvier. Upper Eocene, Debruge (Vaucluse). *A*, Upper cheek teeth. *B*, Lower cheek teeth. 3/4.

The *Xiphodontidae* are slender- and long-footed Selenodonts. In their entire habit they most resemble the ruminants, especially the *Tragulidae* and deer. The genus *Dichodon* has typically ruminant cheek teeth, and is distinguished from all other Selenodonts by the similarity of the posterior premolars to the true molars.

Amphimeryx Pomel (*Hyaegulus* Pomel; *Xiphodontherium* Filhol). Attains the size of *Tragulus*. *Xiphodon* Cuvier (Figs. 247, *D*, 249). Of about the size of a deer, have five crescents in the superior molars.

Dichodon Owen. Superior molars are only quadricrescentic. Premolars simple, the first caniniform, far from the second. Lower jaw low. Oligocene

(Headon beds), Hampshire. *D. cuspidatus* Owen. Eocene Bohnerz of Switzerland. *D. mulleri* Rütimeyer. *D. solodurensis* Stehlin.

Family 8. Caenotheriidae Cope.

Superior and inferior molars selenodont, quinquetubercular; crescentic intermediate cusps in the posterior half in superior molars. Tympanic bullae inflated and filled with cancellated bony tissue. Feet short, tetradactyl; lateral digits slender, considerably shorter than median ones, and not reaching the ground. Upper Eocene, Oligocene and Lower Miocene; Europe.

Fig. 250.

Caenotherium elongatum Filhol. Upper Eocene (Phosphorites), Escamps (Lot). *A*, Skull and lower jaw, lateral aspect. *B*, Skull, upper aspect. $^2/_3$. *C*, Upper cheek teeth. *D*, Lower teeth. $^1/_1$.

The two genera *Caenotherium* Bravard (*Microtherium* Meyer) (Fig. 250) and *Plesiomeryx* Filhol (Fig. 251) are very closely related. The species were only about twenty centimetres high, and evidently lived in large herds.

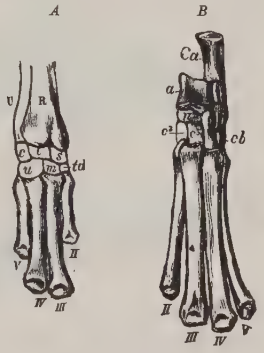


Fig. 251.

Plesiomeryx cadurcensis Gervais. Upper Eocene (Phosphorites), Quercy. *A*, Fore foot. *B*, Hind foot. $^4/_5$. (After Schlosser.) The bones without shading are restored.

Their remains are especially abundant in the Quercy Phosphorites, and in the Lower Miocene of Auvergne and the Mayence Basin. *Oxacron* Filhol, from the Phosphorites, has short robust extremities.

Family 9. Agriochoeridae Leidy.[1]

Dentition usually complete, in a continuous series or with diastema. Dental

[1] *Leidy, J.*, Proc. Amer. Philos. Soc., Philad., 1848, p. 47; *Ibid.*, 1850, p. 121; *Ibid.*, 1851, p. 239.—Jour. Acad. Nat. Sci., Philad., 1869, vol. vii., pp. 71, 131.—*Cope, E. D.*, Proc. Amer. Philos. Soc., Philad., 1884, vol. xxi., pp. 503-512.—*Douglass, E.*, Merycochoerus. Ann. Carnegie Mus., vol. iv., 1907.—*Matthew, W. D.*, Memoirs Amer. Mus. Nat. Hist., New York, vol. i., part vii., 1901, pp. 395, 420.—*Scott, W. B.*, Beitrage zur Kenntniss der Oreodontidae. Morph. Jahrb., vol. xvi., 1890.—On the Osteology of Agriochoerus. Proc. Amer. Philos. Soc., Philad., 1894, p. 243.—*Thorpe, M. R.*, John Day Promerycochoeri. Amer. Jour. Sci., ser. 5, vol. i., 1921.—*Wortman, J. L.*, On the Osteology of Agriochoerus. Bull. Amer. Mus. Nat. Hist., New York, 1895, pp. 145, 178.

formula : $\frac{3.1.4.3.}{3.1.4.3.}$ *Cheek teeth selenodont. Superior molars with four, rarely with five crescents. Premolars anteriorly monocuspid, laterally compressed, slightly elongated, progressively complex posteriorly. Fourth premolar sometimes molariform; inferior first premolar functioning as canine, inferior canine functioning as fourth incisor. Radius, ulna, carpals, tarsals and metapodials distinct. Feet tetradactyl; in more primitive forms, a small pollex in the fore foot.*

The *Agriochoeridae* (*Oreodontidae*) are extinct and at present are known only from the Eocene, Oligocene, Miocene and Pliocene of North America. They have transmitted no descendants to recent times, but probably may be traced back to the same stem-form as the *Camelidae*.

Subfamily 1. Agriochoerinae Leidy.

Superior molars with deeply concave external crescents. Humerus strongly expanded distally, with low trochlea. Terminal phalanges claw-like. Tail long.

In appearance the *Agriochoerinae* show great similarity to the *Anoplotheriidae*, from which they differ by the presence of two lateral toes. Upper Eocene to Lower Miocene: North America.

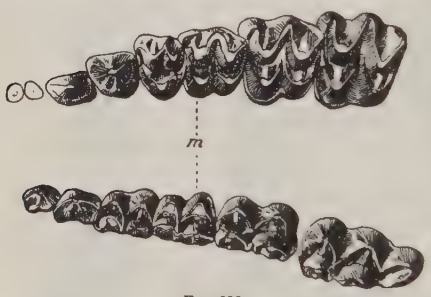


Fig. 252.

Agriochoerus latifrons Leidy. Oligocene (White River beds), Nebraska. Upper and lower cheek teeth. 3/4. (After W. B. Scott.)

Protagriochoerus Scott. Premolars: $\frac{4}{4}$. Superior molars with three crescents in the anterior half of the tooth. Fourth premolar simple in both jaws. Upper Eocene (Uinta beds); *P. annectens* Scott.

Agriochoerus Leidy (*Artionyx* Osborn and Wortman; *Merycopater*, *Coloreodon* Cope; *Agriomeryx* Marsh) (Fig. 252). Dental series broken by a post-canine diastema; without superior incisors. Premolars: $\frac{4-3}{4.}$. Posterior premolar above and below like first molar. Superior molars with four crescents and concave distinctly W-shaped ectoloph. Orbits open posteriorly. Pollex present. Terminal phalanges short, curved and pointed. Oligocene; North America. *A. latifrons*, *major* Leidy, *A. guyotianus* Cope.

Subfamily 2. Oreodontinae Leidy.

Without long diastema. Thorax large, limbs short. Orbits generally closed posteriorly. Humerus typically artiodactyl. Terminal phalanges generally developed into short narrow hoofs.

In habit the *Oreodontinae* exhibit great similarity to *Dicotyles*; the later forms often acquire similarity with *Hippopotamus* by the thickness and prominence of the zygomatic arch. Upper Eocene to Upper Miocene; North America.

Protoreodon Scott and Osborn (*Eomeryx*, *Hyomeryx* Marsh). Dental series continuous. Superior molars very short crowned with three crescents in the anterior and two in the posterior half of the tooth. All premolars monocuspid or bicuspid. Orbits open posteriorly. Upper Eocene (Uinta beds); Wyoming. *P. parvus* Scott.

Limnenetes and *Bathygenys* Douglass. Similar to *Oreodon*, but with orbits open behind. Lowermost White River beds.

Oreodon Leidy (Figs. 253, 254). Dental series continuous. Orbits closed posteriorly. Lachrymal fossae large. Manus with fifth metacarpal, the pollex very short, vestigial. Second and fifth metacarpals shorter than the two median metacarpals. Pes tetradactyl. Exceedingly abundant in the White River Oligocene; North America. *O. culbertsoni*, *major*, *gracilis* Leidy.

Eporeodon Marsh (*Eucrotaphus* Leidy). Skull elongated. Manus without pollex. Lower Miocene (John Day beds); Oregon and Colorado.

Mesoreodon Scott. Crowns of teeth rather high. Allied to *Eporeodon*. Lower Miocene; Deep River beds.

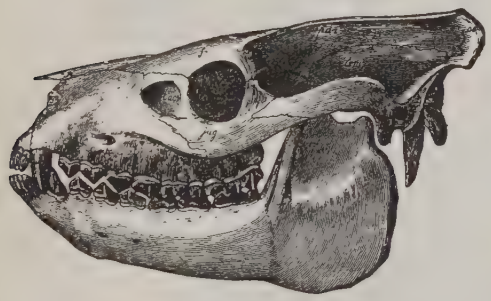


FIG. 253.

Oreodon culbertsoni Leidy. Oligocene (White River beds), Nebraska. Skull and lower jaw. 2/5. (After Gaudry.)

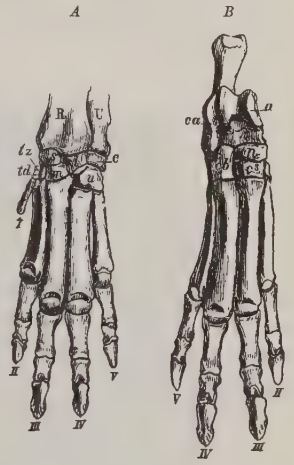


FIG. 254.

Oreodon culbertsoni Leidy. Oligocene (White River beds), Nebraska. *A*, Fore foot. *B*, Hind foot. 1/3. (After W. B. Scott.)

Merycochoerus Leidy. Oreodont-like, but with shorter skull. Zygomatic arch stronger and projecting further. Muzzle broad; nasals shortened. Premolar series short. Skeleton more robust and massive. Upper Miocene (Loup Fork beds); North America. *M. proprius* Leidy.

Promerycochoerus Douglass (Figs. 255, 256, 257). Skull and premolar series long; nasals unreduced. Zygomatic arch thickened posteriorly. Lower Miocene (John Day beds); Oregon. *P. superbus* Leidy (Fig. 255, *B*). Miocene; Nebraska. *P. carrikeri* Peterson.

Pronomotherium Douglass (Fig. 258). Skull extremely short. Premaxillaries united, with spout-shaped depression. Nasals short. Mandible heavy and extremely large and deep. Incisors small. *P. laticeps* Douglass. Upper Miocene; Montana.

Phenacocoelus Peterson. Two elongated and narrow foramina at anterior portion of frontals; cranium long; face short, large tympanic bulla. *Leptau-*

chenia-like in a number of characters. Lower Miocene; western Nebraska. *P. typus* Peterson.

Merychyus Leidy (*Ticholeptus* Cope). Muzzle shortened; vacuity between

FIG. 255.

A, Promerycochoerus macrostegus Cope sp. Skull, lateral aspect. *B, Promerycochoerus superbus* Leidy sp. Skull, palatal aspect. Lower Miocene (John Day beds). Oregon. 1/4. (After Cope.)

lachrymal, maxillary and frontal bone. Molars hypsodont. Lateral digits more reduced than in *Oreodon*. Middle Miocene to Pliocene.

Leptauchenia Leidy. Dental crowns high. Muzzle shortened. Only

FIG. 256.

Promerycochoerus carrikeri Peterson. Miocene, Nebraska. Group of three skeletons in rock. 1/25. (After Peterson.)

Reproduced by permission from The Memoirs of the Carnegie Museum.

two lower incisors present. Zygomatic arch elevated. Upper Oligocene (White River beds); North America.

Cyclopidius Cope (*Pithecistes* Cope). Skull flat, and more strongly modified. Premaxillary distinct, with facial vacuity. Zygomatic arch extending far out from the skull. Middle Miocene (Deep River beds); North America.

FIG. 257.

Promerycochoerus carrikeri Peterson. Skeleton restored by O. A. Peterson. 1/18.
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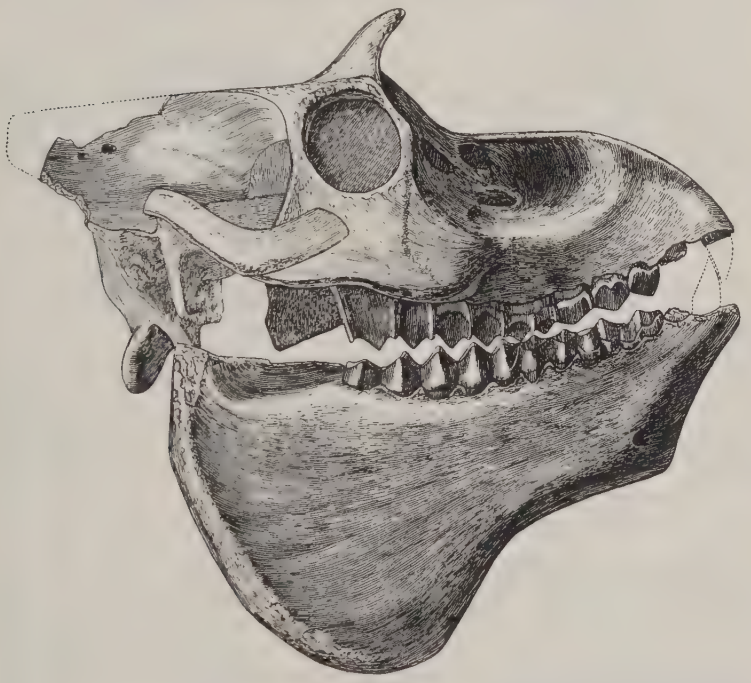


FIG. 258.

Pronomotherium laticeps Douglass. Upper Miocene (Loup Fork beds), Montana. Skull and lower jaw, lateral aspect. 3/8. (After Douglass.)
Reproduced by permission from The Memoirs of the Carnegie Museum.

Family 10. **Camelidae** Gray.[1]

(*Tylopoda* Illiger.)

Dentition more or less nearly complete. Dental formula: $\frac{3\text{-}1.1.4\text{-}2.3.}{3.\quad 1.4\text{-}1.3.}$. *Cheek*

[1] *Cope, E. D.*, The Phylogeny of the Camelidae. Amer. Naturalist, 1886, p. 611.—*Douglass, E.*, Procamelus and Stenomylus. Ann. Carnegie Mus., vol. v., 1908.—*Hay, O. P.*, Camelops.

teeth selenodont, longer than broad, usually separated from canine and frequently from first premolar, by a diastema. Premolars greatly reduced, the first caniniform when present. Cervicals without vertebrarterial canal. Carpals distinct; in the tarsus only second and third cuneiforms coalesced. Feet four- to two-toed, in later forms lateral digits completely atrophied. Principal metapodials with distal median ridges sharply limited to palmar face, as a rule co-ossified, distinct only in the oldest forms. Stomach with three compartments.

Of the two existing genera, *Camelus* and *Auchenia*, the former at present inhabits Asia and northern Africa, and *Auchenia* is limited to South America. The family originated in North America, and in the Eocene, Oligocene and Miocene was wholly confined to this region. In the Pliocene it extended as far as Asia, and thence into northern Africa. The extinct North American types form a continuous evolutionary series, and are traceable back to the primitive unspecialised tetradactyl Eocene forms with separate metapodials and complete dentition.

The skull bears neither horns nor antlers. Its low elongated form, obliquely sloping muzzle, short premaxillary with high ascending branch, the prominent orbits completely surrounded by bone, and the slight inclination of the facial axis toward the cranial axis, lend to it a certain physiognomic similarity to that of the horse. The dentition recalls that of the ruminants, although the molars are narrower, and in the upper jaw there is at least one incisor and a canine, and sometimes all three incisors are present. The premolars are much reduced.

It is noteworthy that notwithstanding the early appearance of coalescence of the metapodials, the carpals and tarsals always remain distinct. In the carpus the trapezoid has been removed to one side and backward by the remarkable broadening of the magnum, yet is still supported by the third metacarpal. In later forms the trapezium is suppressed. Median keels are absent on the dorsal side of the distal articular surfaces of the metapodials. As regards their dental and skeletal development, fossil camels form a conspicuous and peculiar series, the older members of which may be compared in certain particulars with the embryos of the existing genera *Camelus* and *Auchenia*.

Subfamily 1. Leptotragulinae Cope.

Dentition complete, without diastema, brachyodont. Canine larger than third incisor. With the exception of the last, premolars trenchant. Superior molars all with cusps selenoid. Roof of skull flat. Muzzle short. Metapodials not fused together. Manus tetradactyl. Pes with two digits and with proximal splint bones. Radius and ulna anchylosed in adults only. Upper Eocene (Uinta beds) and Oligocene; North America.

Bunomeryx Wortman. Superior molars quinquetubercular: $\frac{4}{3}$. *P. M.* similar to those of *Homacodon*, but selenodont. Uinta beds. *B. elegans* Wortman.

Proc. U.S. Nat. Mus., Washington, vol. 46, 1913.—*Matthew, W. D.*, Memoirs Amer. Mus. Nat. Hist., New York, vol. i., 1901, pp. 420-439.—*Peterson, O. A.*, Oxydactylus. Ann. Carnegie Mus., vol. ii., 1904.—Stenomylus. *Ibid.*, vol. iv., 1908.—Miocene Camel from Nebraska. *Ibid.*, vol. vii., 1911.—*Scott, W. B.*, On the Phylogeny of Poebrotherium. Journ. Morphology, vol. v., 1891, p. 1.—The Selenodont Artiodactyla of the Uinta Eocene. Trans. Wagner Free Inst. Sci., Philad., 1899.—*Wortman, J. L.*, The Extinct Camelidae of North America. Bull. Amer. Mus. Nat. Hist., New York, 1898, pp. 93-142.

Leptotragulus Scott and Osborn (*Parameryx* Marsh). Imperfectly known. Uinta and Titanotherium beds.

Protylopus Wortman. Roof of skull flat. Muzzle and premaxillary short. Orbits not closed behind. Uinta beds. *P. petersoni* Wortman.

Oromeryx Marsh. Uinta beds. *Eotylopus* Matthew. Oligocene (Titanotherium beds).

Subfamily 2. POËBROTHERIINAE Cope.

Dentition complete, brachyodont. Orbits not always closed behind. Premaxillary and symphysis elongated. Radius and ulna coalesced. Metapodials distinct. Pes with two digits, the lateral metapodials consisting of proximal vestiges only, separate or fused to median digits. Terminal phalanges hoof-shaped. Oligocene and Lower Miocene; North America.

FIG. 259.

Poëbrotherium wilsoni Leidy. Oligocene (White River beds), Nebraska. *A*, Skull and lower jaw. 2/5. *B*, Fore foot. *C*, Hind foot. 1/3. (After Wortman.)

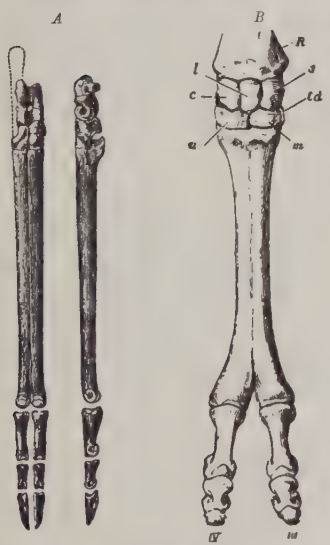


FIG. 260.

A, Hind foot of *Poëbrotherium* (after Cope) for comparison with *B*, fore foot of *Camelus* (after Flower). 1/8.

Poëbrotherium Leidy (Figs. 259, 260, *A*). Inferior canine small. Lateral vestigial metatarsals separate. Size about that of a roe deer. White River beds. *P. wilsoni* Leidy.

Paratylopus Douglass (*Gomphotherium* Cope) (Fig. 261). Inferior canine large.

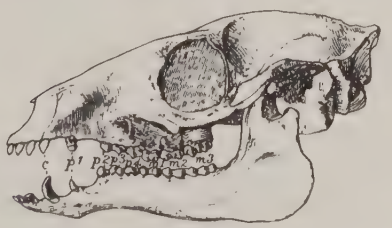


FIG. 261.

Paratylopus sternbergi Cope sp. Lower Miocene (John Day beds), Oregon. Skull and lower jaw. 1/4 (After Wortman.)

Orbits nearly closed. Face shortened. Size that of a wild sheep. John Day and Protoceras beds.

Oxydactylus Peterson. Orbits closed. Lateral vestiges fused to metapodials. Miocene (Upper Harrison beds); Nebraska.

Subfamily 3. Protolabinae Cope.

Cheek teeth hypsodont. Orbit completely surrounded by bone. Radius and ulna coalesced. Feet with two digits; lateral metapodials vestigial, fused, principal metapodials usually fused into a cannon bone. Between the llama and camel in size. Miocene and Pliocene; North America.

Protolabis Cope. Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. First premolar sometimes absent. Metapodials not wholly anchylosed. Upper Miocene (Loup Fork beds); North America. *P. angustidens, heterodontus* Cope, *longiceps* Matthew.

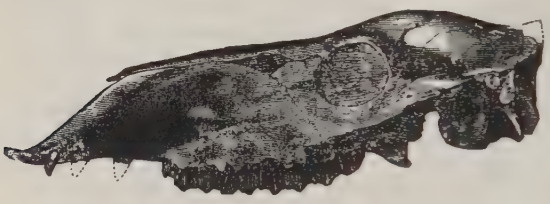


Fig. 262.

Procamelus occidentalis Leidy. Lower Pliocene, New Mexico. Skull. 1/4. (After Cope.)

Procamelus Cope (Fig. 262). Dental formula: $\frac{1.1.4.3.}{3.1.4.3.}$. Metapodials fused. Loup Fork beds. *P. occidentalis, robustus, gracilis* Leidy.

Pliauchenia Cope. Without second premolar. Upper Miocene (Loup Fork beds) and Pliocene; North America; *P. spatula* Cope, *gigas* Matthew and Cook, *vera* Matthew.

Alticamelus Matthew. Without first and second superior incisors, but with four premolars in both jaws. Neck, metapodials, femur and tibia very long. Loup Fork beds; Colorado. Pliocene; Nebraska.

Subfamily 4. Stenomylinae Matthew.[1]

Incisors and canine forming a continuous closed series. Premolars much reduced; lower canine and first premolar caniniform. Molars long, narrow and hypsodont. Orbit large, placed well back and closed posteriorly. Vomer, pterygoid processes of palatines, presphenoid consolidated, forming a heavy convex ridge, interrupting the backward passage of the posterior nares. Coronoid process small and displaced excessively backward. Pes with two digits, the lateral metapodials consisting of sesamoid-like vestiges. Terminal phalanges small, hoof-like. Lower Miocene; North America.

Stenomylus Peterson. Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. Premolars much reduced. Large neck, long and slender limbs, size that of a sheep. Lower Miocene; western Nebraska. *S. gracilis* Peterson.

[1] *Peterson, O. A.*, Ann. Carnegie Mus., vol. iv., 1906-8, pp. 41, 286-300; vol. vii., 1911, pp. 267-273.—*Matthew, W. D.*, Bull. Amer. Museum of Nat. Hist., vol. xxvii., 1910, p. 42.—*Loomis, F. B.*, Amer. Jour. Sci., vol. xxix., 1910, pp. 297-323.

Subfamily 5. Camelinae Cope.

Dentition more or less reduced. Radius and ulna coalesced. Pes with two digits, metapodials anchylosed. Phalanges with rugose under surfaces for attachment of heavy pads. Pliocene and Pleistocene; North and South America. Lower Pliocene, India and China. Pleistocene; Asia and S. Europe. Recent in central and western Asia, northern Africa and South America.

Camelus Linn. (*Merycotherium* Bojanus) (Figs. 260, *B*,2 63). Dental formula: $\frac{1.1.2.3.}{3.1.3.3.}$ Milk dentition of the upper jaw still includes all three incisors; in the permanent dentition, the two anterior incisors are reduced and the third has become caniniform. The superior canine is separated from the third incisor and from the anterior conical premolar by a wide interval, and a diastema likewise follows the first premolar. The two posterior premolars consist of an ectoloph and an internal crescent. Molars rather deep. Inferior incisors spatulate. Canine powerfully developed. Living in northern Africa and Asia. Fossil in the Lower Pliocene of India and China. *C. sivalensis* Falconer and Cautley. Pleistocene; Siberia, southern Russia, Roumania. *C. sibiricus* (Bojanus), *C. alutensis* Stefanescu. Algiers, *C. thomasi* Pomel. Pleistocene; North America. *C. americanus* Wortman.

Fig. 263.

Camelus bactrianus Erxl. Recent, Central Asia. Skull. 1/6. (After Giebel.)

Protauchenia Branco. *Palaeolama* Gervais, *Hemiauchenia*, *Stilauchenia*, *Lamaops* Ameghino. Pampas formation and Pleistocene; South America.

Auchenia Illiger. Dental formula: $\frac{1.1.2.3.}{3.1.1.3.}$ Dentition reduced. Digits distinct. Pleistocene and Recent; South America.

Camelops Leidy. *Holomeniscus* and *Eschatius* Cope. Very closely allied to *Auchenia*, but lacking the antero-external buttress on lower molars. Lowest Pleistocene (Equus beds); Oregon, California (Rancho La Brea) and Mexico.

Family 11. **Tragulidae**, Milne-Edwards.[1] Chevrotains.

Skull without horns. Dental formula: $\frac{-0.1.4-3.3.}{3.1.4-3.3.}$ *Incisors absent in upper jaw. In male, superior canine sabre-like, inferior canine functioning as incisor. Diastema rather long. Molars selenodont, low; superior molars completely surrounded by cingulum, sometimes quinquetubercular. Premolars elongated, laterally compressed, with trenchant crown. Carpals and tarsals partially coalesced. Median*

[1] *Milne-Edwards, A.*, Ann. Sci. Nat. Zool., ser. 5, vol. ii., 1864.—*Kowalevsky, W.*, Gelocus. Palaeontogr., vol. xxiv.

metapodials much stouter than the completely developed lateral ones, distinct or fused into a cannon bone. Reduction of lateral digits adaptive. Stomach with three compartments.

To the *Tragulidae* belong only small forms, the largest of which attain the size of the roe-deer. They appear in the Oligocene of Europe, and are the descendants of *Dichobune*-like forms. In the Miocene they are still rarer and represented only by the genus *Dorcatherium*, the ancestor of *Hyaemoschus* now living in western Africa. The ancestor of *Tragulus*, now living in southern India and the Malayan Islands, still remains to be discovered.

The delicate chevrotains occupy a position intermediate between the *Dichobunidae* and *Cervidae*. Their hornless skull, distinct bones in the forearm, incomplete fusion of the principal metapodials, presence of lateral metapodials, and the elongated trenchant premolars are all primitive characters. On the other hand, the cheek teeth so closely resemble those in the *Cervidae* that only by the closest scrutiny are they distinguishable, being somewhat more robust and less complex in structure. The suppression of the superior incisors is also a distinctly ruminant character. In the two existing genera, the diffuse placenta and the stomach with three compartments prove that in their differentiation, at least, the *Tragulidae* are less progressive than the ruminants, and constitute an independent group beginning in the Oligocene. In special development they are nearly allied to the *Cervidae*, while the *Gelocinae* represent the ancestors of some Old World *Cavicornia* and all *Cervicornia*, with which they are connected by the hornless genera *Amphitragulus* and *Dremotherium*. The geographical range of the *Tragulidae* is limited to the Old World; Europe, Africa, and Asia.

Subfamily 1. Tragulinae.

Occiput high and narrow. Tympanic bullae filled with cancellated bony tissue. Premolars simple, elongated. Inferior molars with oblique ridges running downward from the apex of the protoconid, usually also with ridge on the metaconid. Superior molars with strong cingulum; lateral metapodials complete in manus and pes. Cuboid, navicular, and later also the cuneiforms fused into one bone.

Fig. 264.

Dorcatherium naui Kaup. Lower Pliocene, Eppelsheim, Hesse Darmstadt. Skull and lower jaw. 1/3. (After Kaup.)

Fig. 265.

Dorcatherium crassum Lartet sp. Upper Miocene, Günzburg. *A*, Upper P^3, M^2, M^3. *B*, Lower P_3, M_1, M_2. 1/1.

Fossil in the Oligocene, Miocene and Lower Pliocene of Europe, and in

the Pliocene and Pleistocene of southern Asia. Living in southern Asia and western Africa.

Cryptomeryx Schlosser. Premolars: $\frac{3}{4}$. Superior molars quinquetubercular; inferior molars with ridge close to metaconid. Oligocene; Quercy Phosphorites.

Lophiomeryx Pomel. Superior molars quadritubercular; inferior molars without ridge, with conical metaconid. Metapodials distinct. Oligocene; Cournon, Frankfurt-am-Main, and Quercy Phosphorites.

FIG. 266.

Dorcatherium crassum Lartet sp. Miocene, Heggbach, Würtemberg. Two last milk-molars and the molars of the lower jaw. $\frac{1}{1}$. (After Steinmann and Döderlein.)

Dorcatherium Kaup (Figs. 264, 265, 266). Premolars: $\frac{3}{4}$. Superior molars quadritubercular; inferior molars with ridges on the metaconid and protoconid. Superior canine dagger-shaped. Anterior metapodials distinct; posterior metapodials coalesced; lateral metapodials much attenuated. Miocene; Europe. *D. crassum* Lartet, *D. guntianum* Meyer. Lower Pliocene; Europe, *D. naui* Kaup. India, *D. majus* Lydekker.

Hyaemoschus Gray. Premolars: $\frac{3}{3}$. Living in western Africa.

Tragulus Brisson (Fig. 226, *D*). Very similar to *Dorcatherium*, but much smaller, and median metacarpals and metatarsals anchylosed in the adult condition. Pliocene and Pleistocene; southern India. *T. sivalensis* Lydekker. Living in southern India. *T. menina* Gray.

Subfamily 2. GELOCINAE.

Inferior molars without ridges on protoconid and paraconid. Cuboid and navicular coalesced. Second and third cuneiforms often fused with one another but not with navicular. Median metapodials more or less confluent to form a cannon bone. Lateral metapodials much attenuated and entirely atrophied in the middle.

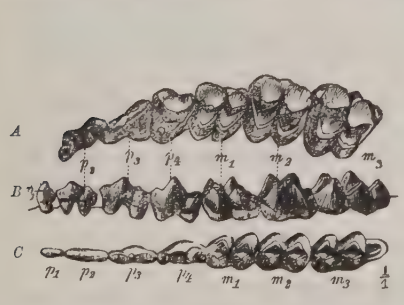


FIG. 267.

Gelocus communis Aymard. Oligocene, Ronzon (Haute Loire). *A*, Upper cheek teeth. *B*, *C*, Lower cheek teeth, outer lateral and upper aspects. *D*, Fore-foot. *E*, Hind-foot. $\frac{1}{2}$. (After Kowalevsky.)

The direct ancestors of the stag and of the *Cavicornia* with stag-like

or ox-like dentition may be expected among the *Gelocinae*. Eocene and Oligocene, and probably in Lower Miocene also; Europe.

Gelocus Aymard (Fig. 267). Superior molars low, with four massive cusps; internal cones of inferior molars robust. Premolars simple, elongated; anterior lower premolar small. Several species of different sizes in the Upper Eocene and Oligocene.

Paragelocus Schlosser. Superior molars quinquetubercular. Oligocene.

Pseudogelocus Schlosser. Premolars complicated. Oligocene.

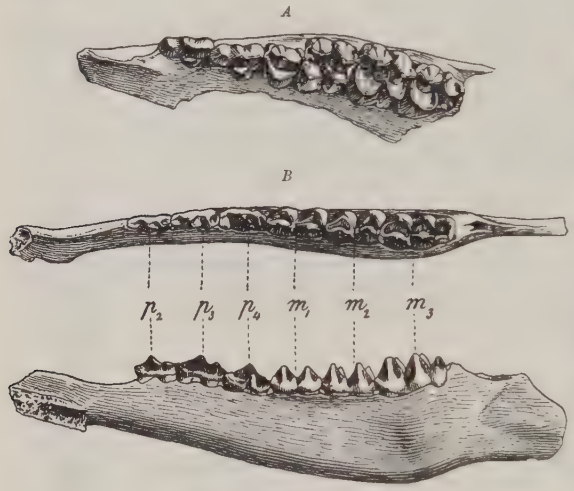


FIG. 268.

Prodremotherium elongatum Filhol. Oligocene (Phosphorites), Quercy. *A*, Upper jaw from below. *B*, Lower jaw from above and inner side. $^3/_4$.

FIG. 269.

Prodremotherium elongatum Filhol. Oligocene (Phosphorites), Quercy. *A*, Metacarpus from behind. *B*, Tibia, tarsus, and metatarsus from front. *C*, Metatarsus from behind. *Ca*, Calcaneum; *F*, rudiment of fibula; *T*, tibia; *a*, astragalus; *cb+sc*, cubo-scaphoid.

Bachitherium Filhol. Premolars: $\frac{3}{3}$. Fourth inferior premolar complicated. Oligocene Phosphorites.

Prodremotherium Filhol (Figs. 268, 269). Premolars: $\frac{3}{3}$, all rather simple. Oligocene Phosphorites.

Family 12. **Hypertragulidae.**[1]

Skull primarily without bony appendages, later with antlers covered with integument. Tympanic bullae often large and hollow. Orbits large, prominent, completely closed posteriorly. Ethmoidal vacuities present. Mandible long and slender. Dental formula: $\frac{3\text{-}0.1\text{-}0.4\text{-}3.3.}{3.\ \ 1.\ \ 4\text{-}3.3.}$ *Inferior canine functioning as fourth incisor. Cheek teeth brachyodont. Inferior molars without fold on posterior part*

[1] *Matthew, W. D.*, Revision of the Hypertragulidae. Bull. Amer. Mus. Nat. Hist., New York, 1902, p. 311. Osteology of Blastomeryx. *Ibid.*, 1908, p. 535.—*Scott, W. B.*, White River Selenodonts. Trans. Wagner Free Inst. Sci., Philadelphia, 1899.

of the protoconid. Superior molars quadricuspid. Premolars simple. Anterior extremity at first tetradactyl, later the lateral toes reduced to distal rudiments. Magnum and trapezoid united. Median metacarpals never united into a cannon bone. Pes with two toes and usually with a cannon bone. Cuboid and navicular co-ossified. Oligocene to Upper Miocene; North America.

The *Hypertragulidae* are confined to North America, where they begin with small forms in the White River Oligocene. They were at first united by systematists with the *Tragulidae*, from which some of the genera differ, however, in the absence of the fold on the metaconid and the protoconid.

Leptomeryx Leidy. $\frac{?\,0\text{-}1.3.3.}{3.\ 1.\ 4.3.}$ Without superior first premolar; inferior first premolar small. Radius and ulna distinct. Oligocene, White River beds. *L. evansi* Leidy.

Hypertragulus Cope. $\frac{?\,1.4.3.}{3.1.4.3.}$ Superior canine and inferior first premolar large, caniniform. Radius and ulna distinct. Extremities as in the foregoing genus. Oligocene (White River beds) to Lower Miocene (John Day beds).

Allomeryx Merriam and Sinclair. Lower Miocene; Oregon. Like *Hypertragulus*.

Blastomeryx Cope (Fig. 270). $\frac{0.1.4\text{-}3.3.}{3.1.4\text{-}3.3.}$ Superior canine elongate. Premolars simple. P_2 and P_3 with small inner tubercle. Inferior premolars with three internal crests separated internally by open valleys. Skull hornless; manus tetradactyl; radius and ulna distinct; pes with two toes and proximal vestiges of lateral digits. Lower Miocene. *B. olcotti* and *B. primus* Matthew. The species described by Scott as *B. gemmifer* Cope is later and generically distinct. It has short antlers and the lateral toes are represented by vestiges.

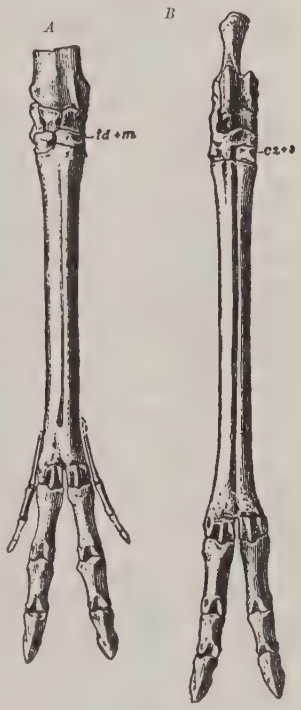


FIG. 270.

Blastomeryx gemmifer Cope. Upper Miocene (Loup Fork beds), Nebraska. *A*, Teleometacarpal fore-foot. *B*, Hind-foot. $^2/_5$. (After W. B. Scott.)

Family 13. Cervicornia. Antlered Ruminants.[1]

Skull of the male as a rule with antlers or bony processes. Dental formula: $\frac{0.0\text{-}1.\ 3.\ 3.}{3.\ 1.\ 3(4).3.}$. *Superior canine either large, protuberant and sabre-like, or weak and*

[1] *Brook, V.*, Classification of the Cervidae. Proc. Zool. Soc., London, 1878, p. 9.—*Dawkins, Boyd*, British Pleistocene Cervidae. Palaeont. Soc., London, 1887.—*Douglass, E.*, Dromomeryx. Ann. Carnegie Mus., vol. iv., 1909.—*Matthew, W. D.*, Osteology of Blastomeryx and Phylogeny of the Cervidae. Bull. Amer. Mus. Nat. Hist., New York, 1908, p. 535.—*Pohlig, H.* Die Cerviden des thüringischen Diluvialtravertins. Palaeontogr., vol. 39, 1892.—*Rütimeyer, L.*, Beiträge zu einer natürlichen Geschichte der Hirsche. Abh. Schweiz. Palaeont. Ges., 1880-83, vols. vii., viii., x.

early deciduous, or entirely wanting; inferior canine incisiform. Diastema wide. Cheek teeth selenodont, low, with several roots. Superior premolars short, with ectoloph and well-developed internal crescent. Carpals (magnum and trapezoid) and tarsals (cuboid and naviculare) partially co-ossified. Principal metapodials (III. and IV.) always fused to form a cannon bone. Lateral metapodials generally much attenuated, either reduced or entirely suppressed, being preserved sometimes as proximal, sometimes as distal rudiments with short phalanges.

As in the *Tragulidae*, the entire skeleton of the *Cervicornia* is characterised by a brittle bony substance with abundant osteoblasts, and by the thin nature of the bones of the skull.

The skull has an elongated subcylindrical form. The cranial and facial axes are nearly in the same line and do not show the strong bending seen in most *Cavicornia*. The arched brain-case is principally formed by the parietal bones, yet the frontals enter into the formation of its narrower portion; laterally the squamosal bones acquire considerable extent. The lachrymal bones are unusually large, and on their facial surfaces have depressions, the so-called lachrymal fossae. Between the lachrymal, nasal, frontal and maxillary bones, there is very frequently an ethmoidal vacuity in the ossification leading into a space filled with thin lamellae of bone and air cavities. The orbits are directed forward and completely surrounded by bone. The most striking feature in the skull of many male deer is the presence of antlers. This character, however, is merely incidental in systematic value, for not only are these osseous structures absent in all females except the reindeer, but in the oldest fossil forms are likewise wanting in both sexes. The presence of antlers also exercises less influence on the general structure of the skull than the horn cores of the *Cavicornia*. Moreover, similar antlered forms are of constant recurrence in various groups of deer not closely related to each other. In the giraffes, *Protoceratinae*, etc., the bony processes on the frontal bones are permanently covered with integument. Usually, however, this skin is gradually worn off by rubbing, leaving the antlers bare. After the rutting season the true antlers are generally shed, thus exposing the basal osseous processes on which they are borne. These are called pedicles. The nodose band at the base of the antlers is known as the burr. In the forms with complex antlers, these begin with a single prong or tine, which in the second year becomes a bifurcated antler; in succeeding years, one new tine is added to those already present. The phylogenetic development also proceeds in a similar manner. Antlers are entirely absent in the oldest Miocene forms. In the Middle and Upper Miocene species of *Palaeomeryx*, they merely consist of a beam with one or two tines; similar also in *Dicrocerus*, but it is shed and renewed. In the Pliocene, the deer start out with a short beam, a longer tine, and from two to three accessory tines. But not until the Upper Pliocene, the Pleistocene and Recent time have antlers displayed that luxuriance, size and abundant branching observed in the stag, reindeer and elk, and most conspicuously in the extinct Irish deer.

In the *Cervicornia* the dentition (Fig. 271) lacks the superior incisors. In the youngest representatives of the deer, the superior canines are also either entirely wanting or appear only in the male and frequently are shed early. The inferior canine has assumed the form and function of an

incisor tooth. The cheek teeth are brachyodont, with several roots; the crowns are covered with thick wrinkled enamel, and as a rule there is a basal pillar between the internal crescents above and the external crescents below. The ectoloph of the superior molars always exhibits two vertical folds, parastyle and mesostyle. Between each external cusp and its corresponding inner crescent there is a pit which shows spur-like processes beginning at the posterior end of that crescent. The superior premolars are very short, and give the impression of being half molars, yet the inner cone does not assume its position through the deformity of a true internal tubercle but through the bending round of the edge of the tooth. The inferior molars are low and typically selenodont; the premolars are slightly elongated and consist of two very nequal segments, a shorter posterior one and a longer anterior one. In the oldest fossil forms there are four premolars present; otherwise there are but three. The posterior upper milk cheek tooth corresponds exactly to the true molars; the two anterior teeth have the elements of the molars, but the internal crescents are somewhat incomplete. The last inferior milk cheek tooth is three-lobed; the two anterior ones are nearly like the teeth replacing them.

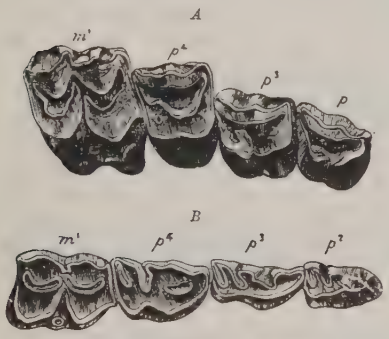


FIG. 271.

Polycladus dicranius Nesti. Upper Pliocene, Val d'Arno, Tuscany. *A*, Three premolars and first molar of upper jaw. *B*, Same teeth of lower jaw. $^1/_1$.

FIG. 272.

Cervus elaphus Linn. Recent. Plesiometacarpal fore-foot. m^2, m^5, Proximal pieces of the lateral metacarpals; *R*, radius. $^1/_7$. (After Flower.)

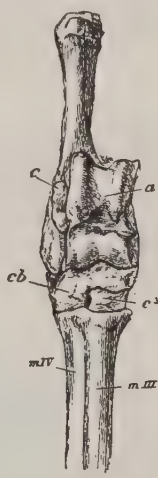


FIG. 273.

Cervus elaphus Linn. Recent. Tarsus and upper end of metatarsus. *a*, Astragalus; *c*, calcaneum; c^3, cuneiform; *cb*, cuboid; *mIII.*, *mIV.*, third and fourth metacarpals. $^1/_3$. (After Flower.)

In the carpus (Fig. 272) the magnum and trapezoid are co-ossified. The median metacarpals are early united into a cannon bone, the lateral metacarpals are exceedingly attenuated, generally rudimentary, sometimes the proximal portions only (*Plesiometacarpi*), sometimes the distal ends only (*Teleometacarpi*), being developed as styloid vestiges. All true deer possess short lateral digits, but these are absent in the giraffe. In the tarsus, as a rule, the cuboid and navicular are united (Fig. 273), as are also the second and third cuneiform bones. The small first cuneiform is always distinct. The lateral metatarsals are present either as short distinct proximal ends, or these may also be firmly co-ossified with the cannon bone. Lateral digits

occur in the typical deer (not in the giraffe), and the lateral metatarsals may also be entirely suppressed.

The geographical range of the *Cervicornia* now extends over Asia, Europe and America, the giraffe also representing this family in central and southern Africa. These forms are therefore wanting only in Australia. In the Old World the plesiometacarpal types predominate; in the New World the teleometacarpal forms. The oldest representatives of the family appear in the Lower Miocene of Europe. In the Upper Miocene and Pliocene, true deer become more widely distributed both in the Old World and in North America. They attained their maximum development in the Pleistocene and Recent.

Subfamily 1. Moschinae Gray. Musk-Deer.

Skull hornless. Upper canine sabre-like, projecting downward. Three premolars present above and below. Distal rudiments of lateral metapodials with long digits having three phalanges.

The two existing genera of this subfamily, *Moschus* and *Hydropotes*, inhabit the highlands of Central Asia. Undoubted fossil remains of *Moschus* have been noted from the Siwalik beds of northern India.

Subfamily 2. Cervulinae Sclater. Muntjacs.

Skull hornless, or in the male with short antlers either only dichotomously branched or with a few tines, these being borne on a long pedicle, and not shed in the old forms. Superior canines very strongly developed, projecting downward, laterally compressed, and trenchant posteriorly. Cheek teeth deer-like; premolars slightly elongated. Manus usually plesiometacarpal, very rarely telecometacarpal. Living in southern Asia. Fossil from the Miocene onward.

Amphitragulus Pomel. Skull hornless, without lachrymal fossa and ethmoidal vacuity. Molars low, nearly smooth, the inferior ones with *Palaeomeryx*-fold on the protoconid. Four inferior premolars, the posterior one elongated. Frequently with distal vestiges of lateral metacarpals and corresponding phalanges. Abundant in the Lower Miocene of Auvergne and in the environs of Ulm and Mayence. *A. elegans*, *lemanensis* Pomel. Miocene; Japan, *A. minoensis* Matsumoto. From about the size of a hare to that of a roe-deer.

Fig. 274.

Dremotherium feignouxi Geoffroy. Lower Miocene, St. Gérand-le-Puy (Allier). Skull. 1/3. (After Filhol.)

Dremotherium Geoffroy (Fig. 274). Like the preceding, but superior molars with more robust tubercles, and only three inferior premolars. Lateral metapodials indicated by proximal splint bones only. Lower Miocene; Auvergne, Ulm and Weissenau. *D. feignouxi* Geoffroy.

Micromeryx Lartet. Small, with rather deep cheek teeth. Upper Miocene; Sansan and Steinheim.

Lagomeryx Roger. Antlers either with simple tines or strongly branched; pedicle long. Size from a hare to a gazelle. Middle Miocene, *L. simplicicornis* Schlosser. Upper Miocene, *L. meyeri* Hofmann. *L. pumilio* Roger.

Palaeomeryx Meyer. Skull probably hornless. Molars with wrinkled enamel. Superior canine large. Inferior molars with strong *Palaeomeryx*-fold. Size from a roe-deer to a red deer. Middle Miocene, *P. annectens* Schlosser. Upper Miocene, *P. bojani*, *P. eminens* Meyer.

Dromomeryx Douglass. Higher, narrower and more modernised teeth than in *Palaeomeryx* of Europe. Upper Miocene (Deep River beds); Montana. *D. borealis* Cope. *D. antilopinus* Scott. *D. madisonius*, *D. americanus* Douglass.

Dicrocerus Lartet (*Procervulus* Gaudry) (Figs. 275, 276). Like *Palaeomeryx*, but skull with bifurcate, rarely three-tined antlers. Upper Miocene; Sansan, Steinheim, etc. *D. elegans* Lartet. In this the antlers are sometimes shed. *D. furcatus* Hensel. With antlers persisting.

Cervulus Blainville. Living in southern India. Fossil in the Pleistocene of India.

Cervavus Schlosser. Antlers branched. Inferior molars often with vestiges of a *Palaeomeryx*-fold. Superior canine rather powerful. Varying in size from the musk-deer to the roe-deer. Lower Pliocene; China. *C. oweni* Koken.

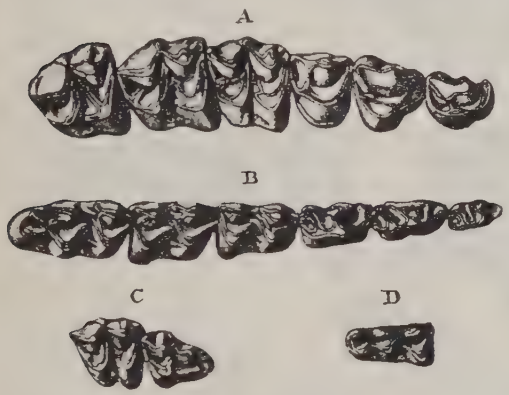


FIG. 275.

Dicrocerus furcatus Hensel sp. Upper Miocene, Steinheim, Württemberg. *A*, *B*, Upper and lower cheek teeth. *C*, Upper milk-teeth (D^3 and D^4). *D*, Lower D_4. 1/1.

FIG. 276.

Dicrocerus elegans Lartet. Upper Miocene, Sansan (Gers). Antler attached to pedicle on cranium. 1/3. (After Gaudry.)

Subfamily 3. CERVINAE Gray.

Antlers with short pedicle, many times branched, periodically shed; as a rule present only in the male, sometimes, however, in both sexes. Superior canine weak or absent. Cheek teeth brachyodont. Manus either plesiometacarpal or teleometacarpal.

Living in the Northern Hemisphere and in South America. With the exception of *Cervus canadensis*, the *Teleometacarpi* represent the New World

deer; with the exception of *Capreolus*, *Alces* and *Rangifer*, the *Plesiometacarpi*, the Old World deer. Fossil from the Lower Pliocene.

Capreolus Hamilton-Smith. Roe-deer. Antlers upright, three-tined. Lower Pliocene; Pikermi, Cucuron and Baltavar. *C. matheroni* Gervais. Middle Pliocene, *C. australis* de Serres, *C. ruscinensis* Depéret. Upper Pliocene; Auvergne. *C. cusanus* Croizet and Jobert. Pleistocene, *C. capreolus* Linn.

Furcifer, *Blastoceras* Gray, *Mazama* Raf. Living and fossil in the Pleistocene of South America.

Odocoileus. Pleistocene and living in North America.

Cervalces Scott. Pleistocene; North America.

Alces Hamilton-Smith. Elk or moose. Living and in the Pleistocene of Europe, northern Asia and North America. In the Lower Pleistocene of Europe. *A. latifrons* Dawkins.

Rangifer Hamilton-Smith. Reindeer. Both sexes with strongly branched recumbent antlers; branches

FIG. 277.

Axis pardinensis Croizet and Jobert. Upper Pliocene, Auvergne. 1/8. (After Gaudry.)

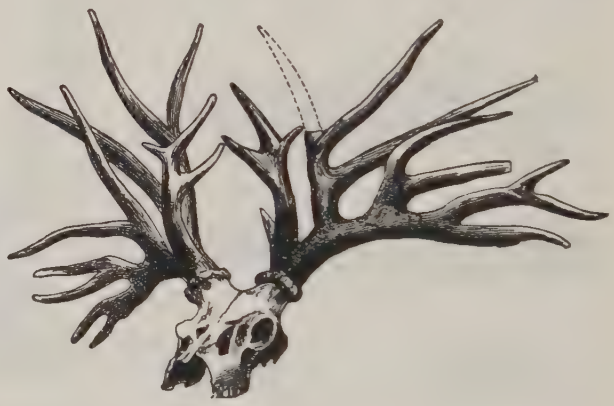


FIG. 278.

Polycladus sedgwicki Falconer. Upper Pliocene, Val d' Arno, Tuscany. Skull with antlers. Greatly reduced.

flattened. The reindeer, *R. tarandus* Linn. sp., inhabits the polar regions of the Northern Hemisphere, and, during the Pleistocene, spread to the Pyrenees and the Alps in Europe. Its remains are found in great quantities in prehistoric settlements of the older Stone Age (Magdalénien stage). In the Pliocene of the Swabian Bohnerz this genus is represented by teeth, and in the Pliocene of Piedmont by antlers. *R. pliotarandoides* de Alessandrini.

Axis Hamilton-Smith (Fig. 277). Antlers slender, with from three to four cylindrical accessory tines. Extremities plesiometacarpal. Living in southern India. Fossil in the Pliocene of Auvergne. *A. borbonicus*, *A. pardinensis* Croizet and Jobert. Crag, England, and Pleistocene of India.

Rusa Hamilton-Smith. Living in Asia. Fossil in the Pleistocene; China. *R. aristotelis* Cuvier.

Cervus Linn (*Elaphus* Gervais). Red deer. Antlers with many tines;

beam and tines cylindrical. Abundant in the Pliocene; Europe. *C. perrieri, arvernensis, issiodorensis* Croizet and Jobert. Pleistocene; Europe. *C. elaphus* Linn. Pleistocene; northern Asia and North America. *C. canadensis.* Similar teeth are also known from the Lower Pliocene of China.

Polycladus Gervais (Figs. 271, 278). Antlers with many tines; branches flattened distally. Pliocene and Lower Pleistocene; Europe. *P. ramosus* Croizet and Jobert. *P. sedgwicki* Falconer.

Megaceros Owen (Figs. 279, 280).[1] Antlers stout, cylindrical at the base, distally flattened and expanded (palmated). Fossil in the Pleistocene and Neolithic; Europe. The largest and most conspicuous species is the Irish elk, *M. hibernicus* Owen, the antlers of which measure from two to three-and-one-half metres from tip to tip. Entire skeletons of *Megaceros hibernicus*, with palmated antlers, are not rare in the peat bogs of Ireland. The females are hornless. Older Pleistocene. *Megaceros euryceros* Aldrovandi.

Dama Hamilton-Smith. Fallow deer.

FIG. 279.

Megaceros hibernicus Owen. Peat bog, Ireland. Skull of female. *A*, Lateral aspect, and *B*, from above. 1/7. (After Owen.)

FIG. 280.

Megaceros hibernicus Owen. Peat bog, Ireland. Skeleton restored by Owen. Greatly reduced.

[1] *Lönnberg, E.*, Taxonomic position of Irish Giant Deer. Archiv för Zoologi, Stockholm, bd. 3, no. 14, 1906.

Antlers cylindrical at base, flattened and expanded distally. Living in southern Europe and Asia Minor. *Dama browni* Dawkins sp. in Pleistocene of southern England.

Subfamily 4. Protoceratinae Marsh.[1]

Dental formula: $\frac{3\text{-}0.1.4.3.}{3.\ 1.4.3.}$. *Superior and inferior canines present in both sexes. Skull long and flat, in late forms with paired bony protuberances. Teeth brachyodont with wrinkled enamel. Carpals distinct. Manus with two stout separate median metapodials and two weaker lateral ones. In older forms, pes with four distinct metatarsals; in later forms, with imperfectly co-ossified cannon bone and proximal lateral splint bones. Tarsals not coalesced.*

The *Protoceratinae* are restricted to North America, but are probably the ancestors of the *Sivatheriinae*.

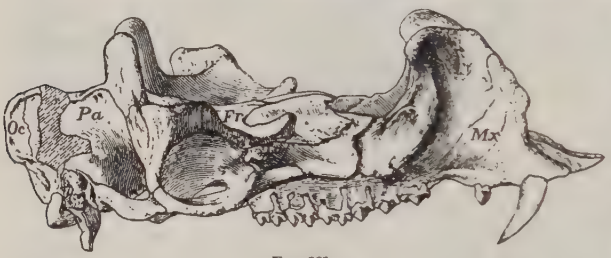


Fig. 281.

Protoceras celer Marsh. Upper Oligocene (White River beds), Nebraska. Skull. 2/5. (After Osborn.)

Camelomeryx Scott. Dental formula: $\frac{2.1.4.3.}{3.1.4.3.}$. Dentition complete. Inferior canine like fourth incisor; first inferior premolar caniniform; superior canine large. Manus and pes tetradactyl, without co-osification of median metapodials. Skull long and flat, without protuberances. Systematic position doubtful. Upper Eocene; Uinta beds.

Leptoreodon Wortman. As *Camelomeryx* but with three upper incisors. Upper Eocene (Uinta beds); Utah.

Heteromeryx Matthew. Skull without bony protuberances. Orbits closed posteriorly. Manus tetradactyl; pes two-toed. Oligocene (Lower White River beds); South Dakota.

Protoceras Marsh (Fig. 281). Dental formula: $\frac{0.1.4.3.}{3.1.4.3.}$. Skull flat; the male with bony bosses on the parietals and frontals and vertical bony plates on the frontals and maxillaries; females with small protuberances on the frontal and parietals only. Manus tetradactyl; lateral digits weaker than median ones. Pes two-toed, with imperfectly united cannon bone and proximal vestiges of lateral metatarsals. Upper Oligocene (White River beds); North America.

Calops Marsh. Skull without bony bosses. Upper Oligocene (White River beds); North America.

Syndyoceras Barbour. Like *Protoceras*, but larger and horn core of proportionally greater size. Lower Miocene; Nebraska. *S. cooki* Barbour.

[1] *Marsh, O. C.*, Amer. Journ. Sci., 1891, p. 87.—*Osborn, H. F.*, and *Wortman, J. L.*, Bull. Amer. Mus. Nat. Hist. New York, 1892, p. 351.—*Scott, W. B.*, Journ. Morphology. Boston, 1895, p. 301.

Subfamily 5. Giraffinae Gray.[1]

Large long-limbed quadrupeds, with elongated skull, either hornless or with short paired simple frontal bosses, without lachrymal fossae, and with small orbits completely surrounded by bone. Bones of cranial roof pneumatic. Superior canines absent; inferior canines bilobate. Cheek teeth low, simple, compressed, deer-like. Lateral metapodials and digits wholly atrophied.

Living in Central Africa. Fossil in the Lower Pliocene of southern Europe, Persia, India and China.

Helladotherium Gaudry (Fig. 282). Skull without frontal protuberances. Neck moderately long. Inferior premolars and molars deep and narrow.

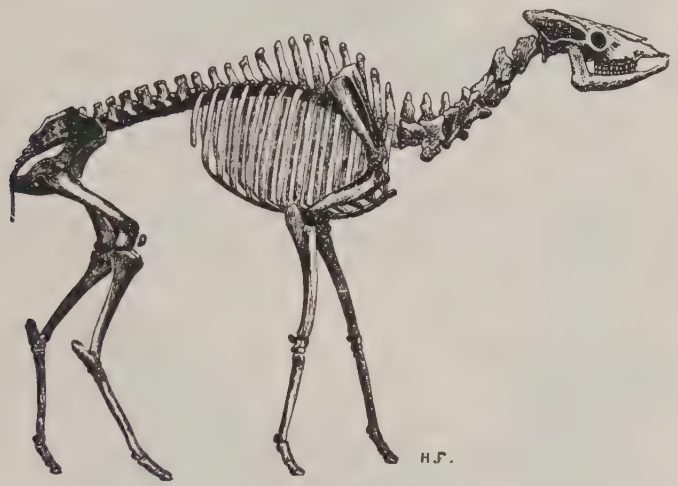


Fig. 282.

Helladotherium duvernoyi Gaudry and Lartet. Skeleton restored by Gaudry. Greatly reduced.

Fore and hind limbs subequal in length. Lower Pliocene; Pikermi, Greece; Veles, Macedonia; Baltavar, Hungary; Taraklia, S. Russia; and Maragha, Persia. A similar but generically distinct skull from the Siwalik probably pertains to *Hydaspitherium grande*, which belongs to the *Sivatheriinae*.

Palaeotragus Gaudry. Skull low, with horns placed far in front. Teeth robust and low. Lower Pliocene; Pikermi.

Samotherium Forsyth Major (*Alcicephalus* Rodler and Weithofer) (Fig. 283). Male skull with a pair of obtuse osseous protuberances above the orbits. Teeth robust and low. Neck shorter and skeleton stouter than in the giraffe. Lower Pliocene; Pikermi, Samos, S. Russia, Persia and China. Essentially identical with *Okapia* living in the Congo forest.

Camelopardalis Schreber. Giraffe. A pair of short bony prominences on the suture between the frontal and parietal bones and a protuberance on the nasal ridge. Premolars very complicated. Molars rather deep.

[1] *Major, C. I. Forsyth*, Okapi, Proc. Zool. Soc. Lond., 1902, pp. 73, 339.

Neck very long. Fore-limbs longer than those behind. Living, and fossil in the Lower Pliocene; Pikermi, Samos, Maragha, Siwalik and China.

FIG. 283.

Samotherium boissieri Forsyth Major. Lower Pliocene, Samos. Skull and lower jaw. 1/6. (After Forsyth Major.)

Subfamily 6. SIVATHERIINAE Gill.[1]

Large ruminants with strongly expanded frontal bone and pneumatic cranial roof. In front of the occipital crest, on the postero-external corners of the frontals,

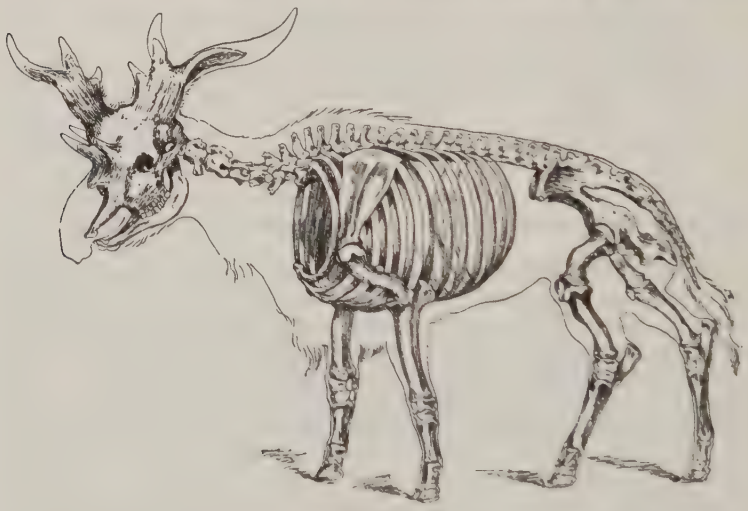


FIG. 284.

Sivatherium giganteum Falconer and Cautley. Lower Pliocene, Siwalik Hills, India. Skeleton restored by J. Murie (*Geol. Mag.*, 1871). Greatly reduced.

two powerful, flattened, slightly branched osseous appendages, borne either on separate

[1] *Abel, O.*, Sivatherium giganteum bei Adrianopel. Sitzb. k. Akad. Wiss. Wien, math.-nat. Cl., Bd. cxiii., p. 1, 1904.

bases or on a common base, with hollow spaces at the base. An additional pair of conical bony prominences sometimes on the anterior portion of the frontal bones. Cheek teeth brachyodont.

All the better known representatives of this family, *Sivatherium* Falconer and Cautley (Fig. 284), *Bramatherium* Falconer and *Hydaspitherium* Lydekker are from the Lower Pliocene (Siwalik beds) of northern India. In the Lower Pliocene of China occur teeth of the *Sivatheriinae*, and from near Adrianople *Sivatherium*-like horn-bosses have been described by Abel.

Family 14. Antilocapridae.[1]

Antlers furcate, enveloped with horny yearly renewed sheath, teeth hypsodont, superior third molar greatly elongated posteriorly. Dental formula: $\frac{3\text{-}0.1.3.3.}{3.\ 1.3.3.}$ Living and fossil in North America.

Hypisodus Cope (Fig. 285). Skull antilopine with elongated parietals. Frontals confined to the supraorbital region. Teeth hypsodont, with long diastema before the second premolar. Canine and first inferior premolar incisor-shaped. Second premolar deciduous. Skull hornless, with large orbits, closed behind; inflated tympanic. Radius and ulna co-ossified. Manus and pes without cannon bone and with complete lateral metapodials. Size of a rabbit. Oligocene (White River beds); North America. *H. minimus* Cope.

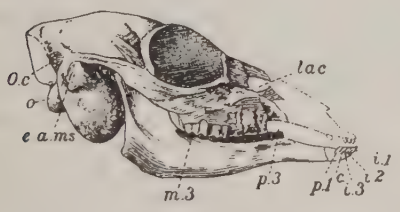


Fig. 285.

Hypisodus minimus Cope. Oligocene (White River beds), Colorado. Skull and lower jaw. 3/4. *e.a.ms*, External auditory meatus; *lac*, lachrymal vacuity; *o*, occipital condyle; *o.c*, supraoccipital. (After Matthew.)

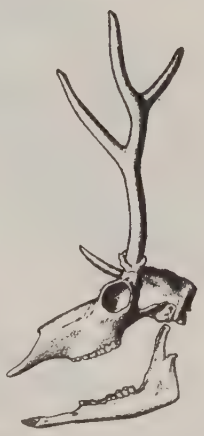


Fig. 286.

Merycodus osborni Matthew. Middle Miocene, Colorado. Skull and lower jaw. 1/4. (After Matthew.)

Merycodus (*Cosoryx*) Leidy (Fig. 286). Antlers with bifurcated branches or with three tines. Cheek teeth hypsodont. Skeleton and teeth Antilocaproid. Manus and pes with cannon bone. Lateral digits represented by short distal vestiges. Upper Miocene, *M. furcatus* Leidy. Middle Miocene, *M. osborni* Matthew. The entire skeleton of the latter is known.

Capromeryx Matthew. With hypsodont molars, and reduced premolars in the lower jaw. Pleistocene of Nebraska.

Antilocapra Ord. Recent, and fossil remains in the Pleistocene.

[1] *Chandler, A. C.*, Notes on Capromeryx, Univ. California Publ. Geology, 1916.—*Lull, R. S.*, New Tertiary Artiodactyls, Amer. Journ. Sci., 1920.—*Matthew, W. D.*, Bull. Amer. Mus. Nat. Hist. New York, 1902, p. 311; 1904, 101.

Family 15. **Cavicornia** Reichenow. Hollow-horned Ruminants.[1]

In both sexes, sometimes only in the male, skull with osseous appendages encased in horn-sheaths. Dentition: $\frac{0.0.3.3.}{3.1.3.3.}$. *Sometimes only two premolars present. Superior incisor and canine teeth absent. Cheek teeth selenodont, brachyodont or hypsodont. Carpus and tarsus as in the Cervicornia. Chief metapodials united into a cannon bone, with sharp distal median keels; lateral metapodials never complete, frequently wholly atrophied. Lateral digits present or absent.*

In comparison with the *Cervicornia*, the *Cavicornia* are seen to be progressive ruminants, in manifold respects highly specialised. In the skull, the facial axis is inclined downward, while the cranial axis is horizontal (Fig. 287). The unusual expansion of the frontal bones, however, lends a still more characteristic appearance to the *Cavicornia*. While the frontal region posterior to the orbits forms the larger portion of the cranial roof, it presses the much reduced parietal bones backward, and in the most extreme forms (*Bos*) these are entirely brought into the occipital surface. With the expansion of the frontals is frequently united a considerable extension of the frontal sinus. The cancellated tissue is replaced by air-cells and the frontal region exhibits a pneumatic condition. In the antelope this peculiar formation of the frontal zone may be traced step by step in its development. While in certain gazelles the frontal bones are still furnished with osseous cancellated tissue, as in the deer, in others larger or smaller air-cavities are present.

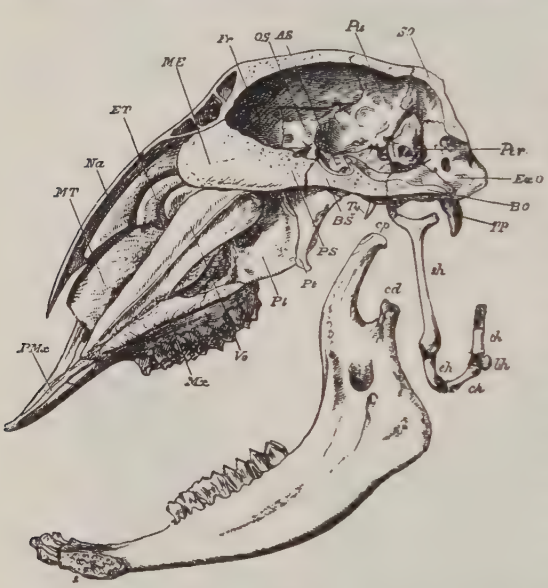


Fig. 287.

Skull of a Hornless Sheep in median vertical section. *AS*, Alisphenoid; *bh*, basihyal; *BO*, basioccipital; *BS*, basisphenoid; *cd*, articular condyle of lower jaw; *ch*, ceratohyal; *cp*, coronoid process of lower jaw; *eh*, epihyal; *ET*, ethmo-turbinal; *Exo*, exoccipital; *Fr*, frontal; *ME*, mesethmoid; *MT*, maxillo-turbinal; *Mx*, maxilla; *Na*, nasal; *OS*, orbitosphenoid; *Pa*, parietal; *Per*, periotic; *Pl*, palatine; *PMx*, premaxilla; *pp*, paroccipital process; *PS*, presphenoid; *Pt*, pterygoid; *s*, symphysis of lower jaw; *sh*, stylohyal; *SO*, supraoccipital; *th*, thyrohyal; *Ty*, styliform process of tympanic; *Vo*, vomer. (After Flower.)

As a rule in both sexes, more rarely only in the male, bony protuberances

[1] *Rütimeyer*, Die Rinder der Tertiarepoche. Abh. Schweiz. Palaeont. Ges., 1877-78.—*Rodler* und *Weithofer*, Die Wiederkäuer der Fauna von Maragha. Denkschr. K. Akad. Wiss. Wien, 1890.—*Schlosser, M.*, Versuch einer Odontographie der Antilopen. Abh. K. Bayr. Akad. Wiss., 1903, p. 161.—Die fossilen Cavicornier der Insel Samos. Beitr. Paläont. Öst.-Ung., xvii., 1904.

arise in the postero-frontal region, above or behind the more or less prominent and entirely closed orbits. These appendages are either solid or more frequently pneumatic in nature, and their hollow bases communicate with the air-cavities in the frontal bones. They are placed between the orbits, and in the more primitive forms are either erect or directed obliquely backward. In the extreme forms (*Bos*) they become displaced backward and outward, and appear on the posterior corners of the skull, being directed nearly at right angles and horizontally outward. The nasal, maxillary and lachrymal bones are generally strongly developed, but the zygomatic arch is slender and short. Lachrymal fossae and ethmoidal vacuities are frequently present in the antelope, but are wanting in the ox, sheep and goat.

The dentition is incomplete and much reduced, especially above, being without incisor and canine teeth. As in all ruminants, the inferior canine stands close to the incisors and functions as such. In the more primitive forms (fossil antelopes) the selenodont cheek teeth remain brachyodont; in the more specialised forms they are hypsodont and at times distinctly prismatic. As a rule the enamel is smooth, more rarely wrinkled. Basal cingula occur only in the antelopes; small accessory pillars are either absent or may become unusually stout (*Bovinae*). In the superior molars the ectoloph comprises two crescent-shaped plates strengthened by vertical folds; the crescentic internal cusps usually form closed pits. The premolars are short, consisting of an ectoloph and one internal crescent. The inferior molars are characterised by their narrowness. The external crescents resemble the internal ones, and the internal cusps the external ones of the superior molars; on the external side an accessory pillar sometimes arises. The three inferior premolars consist of a backwardly sloping crest with expanded processes on the internal side. The incisors, as well as the canine immediately following, have spatulate crowns and differ but little from each other.

The superior milk cheek teeth are somewhat more elongated and irregular than the molars, but usually possess the complete structure of the latter, the foremost only having the anterior half compressed and the posterior half reduced. The last inferior milk cheek tooth is trilobed, while the two anterior are like the teeth replacing them.

The skeleton does not differ essentially from that of the *Cervicornia*. The lateral toes, however, reach an extreme degree of reduction. The median metapodials remain distinct only in the embryonic condition, early uniting to form a cannon bone more or less deeply furrowed anteriorly. Separate proximal vestiges of the two lateral metapodials sometimes continue (antelopes), but generally these also disappear. Lateral digits are frequently present. The carpus and tarsus are constituted as in the deer, likewise the uterus and placenta.

The hollow-horned ruminants form the latest and most abundant group among the ungulates. Not until the Recent period do they attain the maximum point of their development, and by their tendency to modification in breeding show that a certain plasticity and juvenility is inherent in them. It is in the Old World that the *Cavicornia* have chiefly developed and increased. Africa now appears to be their centre of distribution; in truth, however, southern Asia and possibly southern Europe may form the place of origin of the majority of the genera. Yet a certain part of the *Cavicornia* are derived

from the North American selenodont artiodactyls. The previous subdivision of the group into the Antelopes, Ovines and Bovines is not fully justified by the known phylogeny. There is good reason in favour of dividing the extensive tribe of Antelopes into two groups, differing as to characters of the dentition, and to unite these groups with the Ovines and Bovines. This arrangement will then permit us to recognise two large subfamilies, namely: (1) the *Aegodontia*, characterised by hypsodont molars, the upper ones of which are longer than broad; and (2) the *Boodontia*, with cerviform molars, the upper ones being quadrate in outline.

The earliest fossil *Cavicornia* are from the Miocene of Europe. They are deer-like forms possibly having sprung from *Dremotherium*, and representing the ancestral *Boodontia*. These latter attain a great variety of forms in the Pliocene, and are represented in the Pleistocene of North America. During the Pleistocene an immigration took place from Asia into Europe and Africa. The evolution of the group appears to have progressed independently in North America, at least as regards the race of musk-oxen.

Subfamily 1. Aegodontia Schlosser.

Skull almost always arched, frequently with lachrymal fossa or ethmoidal vacuity, or with both, or sometimes with a cleft close to the nasal bones. Parietal bones always entering largely into the formation of the cranial surface. Cranial axis usually bent. Air-cavities generally restricted to the base of the horns, rarely occupying the entire osseous appendages. Horns seldom straight and cylindrical, usually laterally compressed and directed backward, rarely spiral or turned outward, always arising just above the orbits. Molars chiefly hypsodont, seldom with weak basal pillar, as a rule without vertical costae on the external or internal tubercles. Premolars and molars always with enamel smooth.

The *Aegodontia* include the *Neotraginae*, *Gazellinae* (*Antilopinae* of Sclater), *Rupricaprinae*, *Ovicaprinae* and *Ovibovinae*, the first two of which were formerly classed with antelopes in the widest sense. In the structure of the teeth, however, they differ so essentially from the latter forms that their separation seems absolutely unavoidable. On the other hand they exhibit such close relationship to the *Ovicaprinae* that it is probable the three groups have had a common origin. The North American *Antilocapridae* may be regarded as the common ancestral stock, the teeth of which have smooth enamel. In the *Ovicaprinae* and *Gazellinae* (*Antilopinae* of Sclater) the relationship is further emphasised by the fact that both possess relatively long splint bones. These, however, are represented in the former group by scarcely more than the fifth metacarpal. The other *Cavicornia* exhibit the same manner of reduction in the lateral digits as in the deer. Among gazelles reduction of the premolars frequently takes place.

Group 1. Neotraginae Sclater and Thomas.

Skull slightly arched, with lachrymal fossa, without ethmoidal vacuity. Horns cylindrical, inclined backward, tips directed forward. Teeth brachyodont.

Neotragus, *Oreotragus*, *Raphiceros*, *Madoqua* and *Ourebia*. Recent; Africa.

Group 2. GAZELLINAE Coues.

Skull flat or moderately arched, with lachrymal fossa and ethmoidal vacuity. Horns cylindrical or laterally compressed, recurved, only exceptionally spiral, never keeled. Teeth rarely brachyodont, usually strongly hypsodont.

Lithocranius Kohl. Teeth brachyodont. Living in Africa.

Antilope Ogilby. Horns long and spiral. Pleistocene and Recent; India.

Gazella Blainville (Fig. 288). Frontal appendages immediately posterior to the orbits, directed steeply upward or recurved, usually cylindrical, rarely

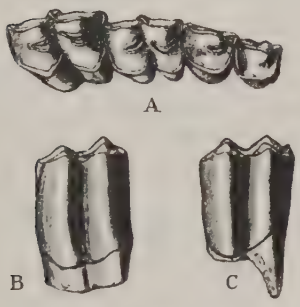


FIG. 288.

Gazella dorcadoides Schlosser. Lower Pliocene, China. *A*, Upper cheek teeth, P^3 to M^2. *B*, Inner aspect of upper molar. *C*, Outer aspect of second lower molar. 1/1.

FIG. 289.

Saiga tatarica Forst. Pleistocene, Twickenham, near London. Frontlet of male. 1/4. (After A. S. Woodward.)

compressed. Lower Pliocene; Pikermi, Concud (Spain), Cucuron, Baltavar, Samos, Maragha, etc., *G. brevicornis* Wagner, *G. deperdita* Gervais. (?) *G. gaudryi* Schlosser. Various species are found in the Lower Pliocene of China and India. Upper Pliocene; Auvergne. *G. borbonica* Bravard. Upper Pliocene; Bresse. *G. burgundica* Depéret. Upper Pliocene; England. *G. anglica* Newton. Pleistocene; Algiers, and living in Asia and Africa.

Saiga Gray (*Colus* Wagner) (Fig. 289). Frontal appendages short, directed steeply upward. Pleistocene; Europe, and living on the steppes of eastern Europe and western Asia.

Pantholops Hodgson. Pliocene; Tibet. *P. hundesiensis* Lydekker. Living in Asia.

Group 3. RUPICAPRINAE Brookes.

Skull arched, rarely flat, with or without lachrymal fossa and fissure-like ethmoidal vacuity. Horns cylindrical, vertical or inclined backward. Teeth moderately hypsodont.

Rupicapra Hamilton-Smith. Recent; Europe and western Asia. Occurs rarely in the fossil state in the European Pleistocene.

Nemorhaedus Hamilton-Smith. Recent; Asia. Upper Pliocene; Sénèze, Haute Loire, France.

Myotragus Bate.[1] Unique among artiodactyl ungulates in having lower incisors reduced to a single pair, persistently growing. Premolars reduced to two above, one or two below. Molars extremely hypsodont. Metapodials and phalanges short and thick. Caverns; Balearic Isles. *M. balearicus* Bate, as large as goat. Probably another species in Caverns of Sardinia.

Group 4. Ovicaprinae Noack.

Skull strongly arched; cranial axis strongly bent. Horns keeled, simply or spirally curved. Frontal appendages usually hollow. Lachrymal fossa small or wanting, ethmoidal vacuity fissure-like or absent. Teeth generally strongly hypsodont and laterally compressed.

Oioceros Gaillard (*Antidorcas* Roth; ? *Helicophora* Lydekker). Lachrymal fossa small; ethmoidal vacuity fissure-like. Horns spiral, keeled. Teeth slightly hypsodont. Lower Pliocene; Pikermi. *O. rothi* Gaudry. Maragha. *O. atropatenes* R. and W. Samos. *O. proaries* Schlosser.

Ovis Linn. (Fig. 287). Lachrymal fossa present; ethmoidal vacuity absent. Frontal sutures converging anteriorly; parietal sutures straight. Frontal processes triangular, broad in front, spiral. Rare in the European Pleistocene. *O.* (or *Caprovis*) *savini* Newton. *O. argalioides* Nehring. In the Pleistocene of Canada, *O. canadensis.* Domestic sheep first appear in Neolithic deposits.

Capra Linn. Lachrymal fossa absent; ethmoidal vacuity fissure-like. Horns compressed, recurved. Frontal sutures straight; parietal sutures converging anteriorly. Pliocene; India. *C. sivalensis* and *C. perimensis* Lydekker. Pleistocene; Europe. *C. pyrenaica* Schimper. *Ibex cebennarum* Gervais. *I. fossilis* Nehring. Domestic goats first appear in Neolithic deposits.

Haploceros Hamilton-Smith (*Oreamnus* Rafinesque). Recent and Pleistocene; North America, caves of California.

Bucapra Rütimeyer. A very large hornless skull from the Pliocene of the Siwalik hills. *B. daviesi* Rüt.

Pseudobos Schlosser. Teeth are known corresponding in size to those of oxen. Premolars reduced. Molars hypsodont, strongly compressed. Lower Pliocene; China and Persia.

Group 5. Ovibovinae Gill.

Skull slightly arched. Horns usually strongly thickened at the base, tips directed outward. Teeth moderately hypsodont; molars strongly compressed.

Ovibos Blainville (*Bootherium* Leidy; *Symbos* Osgood). Musk-ox. Frontal appendages behind the orbits directed downward; tips directed outward; strongly swollen at the base, consisting of cancellated osseous tissue. Metapodials short and thick. *O. moschatus* Blainville now inhabits the most northern portions of North America, particularly Greenland and Alaska; in the Pleistocene it was distributed over a great part of North America,

[1] *Andrews, C. W.*, Phil. Trans. Roy. Soc. Lond., vol. ccvi. B, 1915, p. 281.—Geol. Mag., 1915, p. 337.—*Bate, D. M. A.*, Geol. Mag., 1909, p. 385. *Ibid.*, 1914, p. 337.

Asia and Europe. In the Missouri region it was represented by a second species, *O. priscus* Rütimeyer.

Euceratherium Sinclair. Skull ox-like. Parietal bones displaced to the vertical occipital surface. Horns compressed, far removed from the orbits, with tips directed outwardly. Teeth moderately hypsodont. Pleistocene; California. *E. collinum* Sinclair and Furlong.

Preptoceras Furlong. Similar to *Euceratherium*. Horns circular in section. Pleistocene of California.

Subfamily 2. Boodontia Schlosser.

Skull flat or arched, with or without lachrymal fossa and ethmoidal vacuity, rarely with both. Parietal bones nearly always entering considerably into the formation of the cranial roof; cranial axis more or less bent; air-cavities either absent, or confined to the base of the frontal appendages, or filling a large part of the cranial roof. Horns usually arising near the orbits, only rarely removed far backward, as a rule directed backward, simply curved, or spiral, tips often turned outward. Cross-section of horns circular, more rarely elliptical or keeled. Molars brachyodont or hypsodont, often with vertical costae on the external cusps of the superior molars and on the internal cusps of those below. Basal pillars not rare, especially on superior molars. All molars and premolars with rugose enamel, often with much cement.

The *Boodontia* embrace the *Cephalophinae*, the *Pseudotraginae* (known only in the fossil state), the *Bubalidinae*, *Hippotraginae*, *Cervicaprinae*, *Tragelaphinae* and *Bovinae*. They all originate in forms having teeth very similar to those of the deer, but characterised by somewhat deeper crowns. The *Tragelaphinae* and *Cephalophinae* still remain in this condition; the *Bubalidinae*, *Hippotraginae* and *Cervicaprinae* are very similar to the *Bovinae* in the structure of their teeth, the *Bubalidinae* being distinguished from the latter merely by the absence of basal pillars. Reduction of the premolars occurs rarely. The originally flat elongated skull becomes modified partly through the bending downward of the cranial axis and partly through the change of position of the horns. The parietal bones are thus pressed more and more backward and to the angles, so that they enter only very slightly into the formation of the cranial roof (many *Bubalidinae* and *Bovinae*) or become quite rudimentary (*Bos* and *Bovinae*). The difference between the *Bubalidinae* (heretofore always associated with antelopes), *Hippotraginae* and *Cervicaprinae*, as opposed to the *Bovinae*, consists in the fact that aside from the nature of the horns they never attain more than part of the specialisation characteristic of the *Bovinae*, either in the structure of the teeth or in that of the skull. Only short proximal rudiments of the lateral digits have been found, and these are entirely absent in the *Bovinae*.

The *Boodontia* are an Old World stock, which probably branched off from hornless *Cervicornia* in the Lower Miocene, and are represented in the Upper Miocene of Europe by several forms not particularly well characterised, described as "*Antilope*" *clavata*, *cristata* and *martiniana*, with deer-like dentition, together with the slightly hypsodont genus *Protragocerus*. The organisation of these primitive forms permits them to be considered as ancestors of nearly all later genera.

Group 1. Cephalophinae.

Skull slightly arched; cranial axis not bent downward; lachrymal fossa large,

ethmoidal vacuity absent. Horns short, cylindrical, inclined backward. Molars brachyodont, without basal pillar.

Protetraceros Schlosser. Lower Miocene; China.

Tetraceros Leach. Pliocene to Recent; India.

Cephalophus S. Smith. Recent · Africa. Pleistocene; Algiers.

Boselaphus Blainville (*Portax* H. Smith). This genus, from the Pliocene, Pleistocene and Recent of India, was referred to the *Cephalophinae* by Rütimeyer, but by most other authors is placed in the *Tragelaphinae*. The latter procedure is undoubtedly incorrect. It is preferable to regard this genus as the type of a distinct group, although it certainly displays great similarity to the *Cephalophinae*, from which it differs only in the size of the body, absence of a lachrymal fossa and presence of the hypsodont teeth. At all events it is very closely related to the prototype of the ox.

Paraboselaphus Schlosser. Only detached teeth are known, from the Swabian Bohnerz and from the Lower Pliocene of China.

Group 2. Pseudotraginae Schlosser.

Skull moderately or strongly arched; lachrymal fossa large; ethmoidal vacuity absent. Horns straight or curved, always inclined backward, elliptical or circular in cross-section. Cheek teeth brachyodont or moderately hypsodont, usually with weak basal pillar. Upper Miocene to Lower Pliocene.

This group embraces the oldest *Cavicornia*, but only in part do they appear to have left posterity; at least this is fairly certain in regard to *Pseudotragus*, and is very probable also concerning the other Lower Pliocene genera.

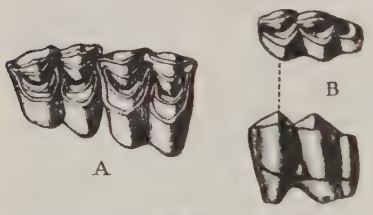


Fig. 290.

Eocerus cristatus Biedermann sp. Upper Miocene, Leoben, Steiermark. *A*, Second and third upper molars, grinding surface. *B*, Third lower molar, grinding surface and outer aspect. 1/1.

Eocerus Schlosser (Fig. 290). Attaining the size of a sheep. Horns straight, strongly inclined backward, circular or elliptical in cross-section. Teeth brachyodont, cervine. Upper Miocene; Sansan, Styria, etc. *"Antilope" martiniana, sansaniensis, clavata* Lartet. *A. cristata* Biedermann. *"Cervus" lunatus* and *C. haplodon* Meyer.

Pseudotragus Schlosser. Presence of a deep lachrymal fossa, horns and skull caproid. Teeth brachyodont. *P. capricornus* Schlosser. Lower Pliocene; Samos.

Pachytragus Schlosser. Cranial axis strongly bent. Horns curved slightly backward, rounded-polygonal in cross-section. Teeth slightly hypsodont. *P. crassicornis* Schlosser. Lower Pliocene; Samos.

Protoryx Forsyth Major. Cranial axis strongly bent. Skull long and narrow. Horns recurved, elliptical in cross-section. Teeth moderately hypsodont. *P. carolinae* Major. Lower Pliocene; Pikermi, Maragha and Samos. Perhaps also in the Pontic limestone of Odessa.

Protragocerus Depéret. Attaining the size of a fallow deer. Horns straight, rounded-triangular in cross-section. Teeth brachyodont. Upper Miocene; La Grive St. Alban, Isère. *P. chantrei* Depéret.

Tragocerus Gaudry (Fig. 291). Skull long and narrow; cranial axis slightly bent. Horns slightly curved, strongly compressed, keeled on the anterior side. Molars subbrachyodont. Lower Pliocene; Pikermi, Cucuron, etc., *T. amaltheus* Wagner sp. A variety occurs also in Samos and Maragha. Lower Pliocene; China, *T. gregarius* Schlosser.

Neotragocerus Matthew. Horn short, straight, oval in section. Molars probably brachyodont. Pliocene; Nebraska.

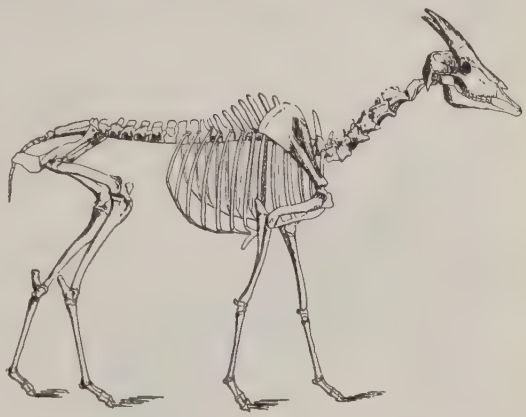


FIG. 291.

Tragocerus amaltheus Wagner sp. Lower Pliocene, Pikermi, Athens. Skeleton restored by A. Gaudry. Much reduced.

Group 3. BUBALIDINAE Sclater and Thomas.

Skull long and slender, with or without lachrymal fossa, without ethmoidal vacuity. Horns pushed far backward, usually roundish in cross-section and more or less spiral. Teeth generally hypsodont, without basal pillar.

Bubalis Cuvier (*Alcelaphus* Blainville). Lachrymal fossa present. Horns short, directed strongly outward; tips directed forward. Fossil in the Pleistocene; Algiers. Recent; Africa.

Damaliscus Sclater. Lachrymal fossa present. Horns long. Parietal bones relatively short. Fossil in the Pliocene; Siwalik Hills, India. *D. palaeindicus* Lydekker sp. Recent; Africa.

Prodamaliscus Schlosser. Parietal bones long. Horns strongly inclined backward. Teeth moderately hypsodont. Lower Pliocene; Samos.

Connochaetes Lichtenstein. Gnu. Skull and horns ox-like. Pliocene; Algiers. In the Pliocene Bohnerz of Swabia are found teeth (*Antilope jaegeri* Rütimeyer), which have some similarity to those of the gnu.

FIG. 292.

Criotherium argaloides Forsyth Major. Lower Pliocene, Samos. Skull. 1/4.

Criotherium Forsyth Major (? *Urmiatherium* Rodler) (Fig. 292). Lachrymal

fossa weak. Parietal bones almost entirely removed to the occipital surface. Excessive development of air-cavities in all bones of the cranium. Horns far back, short, spiral and keeled. Teeth subbrachyodont. Lower Pliocene; Samos, Bessarabia, and Maragha. *C. argalioides* Forsyth Major.

Group 4. Hippotraginae Gray.

Skull long, cranial axis bent. Ethmoidal vacuity present; lachrymal fossa absent. Horns over the orbits curved or straight, always of considerable length, and roundish in cross-section. Teeth hypsodont, with strong basal pillars; in the older forms brachyodont, with only weak basal pillars.

Hippotragus Sundevall. Horns strongly recurved. Teeth hypsodont, with strong basal pillar. Pliocene; India. *H. palaeindicus* Lydekker. Pleistocene; Algiers. Recent; Africa.

Oryx Blainville. Horns long, straight, inclined backward. Teeth with moderate basal pillars. Recent; Africa.

Palaeoryx Gaudry. Horns moderately long, roundish in cross-section, only slightly inclined backward. Teeth brachyodont, with weak basal pillars. Lower Pliocene; Pikermi and Maragha. *P. pallasi* Wagner. Samos. *P. majori* and *P. stutzeli* Schlosser. The former of these species occurs also at Odessa. Middle Pliocene; *P. meneghinii* Rütimeyer, *P. boodon* and *P. cordieri* Gervais.

Tragoreas Schlosser. Horns strongly inclined backward. Lower Pliocene; Samos. *T. oryxoides* Schlosser.

Addax Rafinesque. Horns long and lyrate, spirally curved. Teeth with moderate basal pillars; superior molars with islands of enamel. Recent; Africa.

Plesiaddax Schlosser. Teeth slightly hypsodont, similar to those of *Addax*. Lower Pliocene; China.

Group 5. Cervicaprinae Gray.

Skull moderately long, slightly arched, with ethmoidal vacuity, without lachrymal fossa. Horns rather short, slightly inclined, lyre-shaped. Teeth hypsodont, bovine.

Of the three genera included here, *Pelea* Gray, *Cobus* A. Smith and *Cervicapra* Blainville, the last two are indicated by remains in the Pleistocene of Algiers. Lydekker has described two doubtful species of *Cobus* from the Siwalik Pliocene.

Group 6. Tragelaphinae Jerdon.

Skull long, slightly arched, with ethmoidal vacuity, in the fossil forms with lachrymal fossa also. Horns long, lyre-shaped, keeled, and spiral, roundish in cross-section. Teeth always brachyodont, only in fossil forms with weak basal pillar.

Tragelaphus Blainville; *Strepsiceros* Hamilton-Smith; *Taurotragus* Sclater; *Oreas* Desmarest. Recent in Africa. One species each of *Strepsiceros* and *Oreas* (*S. falconeri* Lydekker and *O. latidens* Lydekker) in the Pliocene of the Siwalik Hills, India. Strepsiceroid teeth occur in the Lower Pliocene of China. *Strepsiceros kudu*, fossil in the Pleistocene of Algiers.

Palaeoreas Gaudry (Fig. 293). Horns with two keels. Parietal bones sloping at an angle toward the occiput. Lower Pliocene; Pikermi and Maragha. *P. lindermayeri* Wagner sp. One species also in China. Pliocene; Auvergne. "*Antilope*" *torticornis* Aymard, perhaps identical with *P. montiscaroli* Major, from Val d'Arno, Italy.

Protragelaphus Dames. Horns with a single keel, roundish in cross-section. Lower Pliocene; Pikermi, Bessarabia, Samos and Maragha.

FIG. 293.

Palaeoreas lindermayeri Wagner, sp. Lower Pliocene, Pikermi, Athens. Skull. 1/3. (After Gaudry.)

Prostrepsiceros Major. Horns with two keels, triangular in cross-section. Lower Pliocene; Maragha, Persia. "*Tragelaphus*" *houtum-schindleri* Rodler and Weithofer.

Helicophora Major. Horns with a single keel, tips directed inward. Lower Pliocene; Pikermi.

Illingoceras Merriam.[1] Horns straight, spiral and keeled. Supposed Pliocene of West Nevada. Systematic position doubtful. *I. alexandrae* Merriam.

Group 7. BOVINAE Gray. Oxen.[2]

Frontal appendages hollow, powerful cylindrical or triangular, usually directed outward at right angles, situated at some distance behind the orbits on the posteroexternal corners of the skull. Frontal bones exceedingly large, reaching to the occiput; parietal bones very short. Cheek teeth prismatic, deep, with strongly developed basal pillars and rather thick layers of cement.

[1] *Merriam, J. C.*, Strepsicerine Antelopes in Tertiary of N.W. Nevada. Univ. California Publ., Bull. Dept. Geol., vol. v., no. 22, 1909.

[2] *Dürst, J. U.*, Notes sur quelques Bovidés préhistoriques. L'Anthropologie, Paris, 1900.—*Rütimeyer, L.*, Versuch einer natürlichen Geschichte des Rindes. Neue Denkschr. Schweiz. Ges. f. Naturw., 1866-67, vols. xxii., xxiii.—*Turner, H. N.*, On the Genera and Subdivisions of the Bovidae. Proc. Zool. Soc. London, 1849.

Oxen are large, robust ruminants in which the characters of the *Cavicornia* have attained their highest development. Their fossil remains first appear in the Pliocene of northern India, afterwards in the Upper Pliocene of Europe. As fossils oxen are not found in great abundance until the Pleistocene, when they had the entire present range of the *Bovinae*.

The frontal bones are filled with air-cavities, become greatly expanded, and form almost the entire roof of the brain-case. In some instances, the parietal bones are quite excluded from the cranial roof, while the more or less outwardly directed frontal appendages are removed far backward and outward. The lachrymal and nasal bones have considerable size, but lachrymal fossae are absent.

Fig. 294.

Bubalus brachyceros Gray. Recent, Africa. Male skull, front and lateral aspects. Greatly reduced. (After Rütimeyer.)

Rütimeyer divides oxen into five groups, as follows:

A. Bubalus Group.
Buffalo.

Frontal region strongly arched, relatively but little expanded; accordingly the parietal bones take some part in the upper surface of the cranial roof. Horn-cores beginning near the median line of the skull. Horns and horn-cores flattened, generally triangular, directed backward and outward. On the inner side of the superior molars are strong basal pillars, variously curved or folded.

Osteologically, buffaloes occupy an intermediate position between oxen and the genus *Boselaphus* Blainville (*Portax* H. Smith). Wild buffalo at present inhabit only southern Asia and Africa.

The extinct genera *Probubalus* Rütimeyer (*Hemibos* and *Peribos* Falconer) and *Amphibos* Falconer are found in the Tertiary of northern India. *Buffelus*

Blumenbach occurs in the Pleistocene of India, and *Bubalus* Rütimeyer (Fig. 294) in the Pleistocene of Europe and Algiers.

B. Leptobos Group.

Skull low, much elongated. Horns arising immediately behind the orbits, bases widely separated, not very powerful, subcylindrical or but little flattened below, directed backward, sometimes entirely absent. Parietal bones relatively large, appearing on the upper surface of the skull.

The single genus *Leptobos* Rütimeyer is found in the Pliocene and Pleistocene of northern India. *L. falconeri* Rütimeyer. According to Forsyth Major, *Bos etruscus* Falconer from the Pliocene of Val d'Arno, Auvergne and Spain, belongs to the genus *Leptobos*. Teeth from the Pliocene Bohnerz of Melchingen may also pertain to this group.

C. Bibos Group.

Posteriorly frontal bones strongly expanded transversely, frontal region much expanded and flat; parietal region distinct only in the young, later excluded from the cranial roof. Horns more or less flattened, situated far back on the fronto-occipital border; in the young directed backward, in the adult laterally.

Recent and fossil representatives of the genus *Bibos* Hodgson are found in southern India, and a Pleistocene species in Java.

D. Bison Group.

Skull low, frontal region flat, unusually broad and relatively short, the cylindrical horns directed outward and upward, and standing a short distance behind the very prominent orbits. Parietal bones short, broad, but always developed on the cranial roof. Facial portion of skull short. Nasal bones short, broad posteriorly.

Two species of this group survive at the present day, the European aurochs, *B. europaeus* Gmelin in Lithuania, and the American bison in North America.

Bison priscus Bojanus sp. is found in abundance in the Pleistocene of Europe and northern Asia. Pleistocene bison are also found in North America, the species being known as *B. antiquus* Leidy and *B. latifrons* Harlan. The fossil European aurochs is more closely allied specifically to the fossil and existing American bison than to *B. europaeus*. The oldest remains of the bison are found in the Upper Pliocene of northern India. *B. sivalensis* Falconer.

E. Taurus Group. Oxen.

Frontal bones enormously expanded, forming the entire cranial roof; parietal bones unusually short and quite excluded from the cranial roof. Position of the horn-cores removed far back to the postero-external angles of the skull.

In this group the structure of the bovine skull has reached the culminating point. The frontal region has gained an extraordinary expansion, and the parietal zone has experienced a reduction seen in no other division of the

ungulates. Feral representatives of this group, which includes the single genus *Bos* Linn. (Figs. 295-297), no longer exist. The domestic ox, *B. taurus* Linn., is now distributed throughout the world, and by breeding has become split up into various races. Rütimeyer distinguishes three races of European oxen. The *Primigenius* or *Trochoceros* race having the greatest similarity to the fossil Urus, *B. primigenius* Bojanus, was evidently derived from it. During the stone age it already had a wide distribution. The *Frontosus* race is

FIG. 295.
Bos primigenius Bojanus. Pleistocene, Scotland. (After Owen.)

FIG. 296.
Bos taurus Linn. (*primigenius* race). Holstein. Female skull. (After Rütimeyer.)

FIG. 297.
Bos taurus Linn. From Swiss Pile-dwelling. *A*, Upper, and *B*, lower molar. 1/1.

characterised by the unusually broad frontal region. It probably developed from the *Primigenius* race, and is first found in the Bronze Age. The *Brachyceros* race has short, strongly curved non-pedicled horn-cores, a long narrow skull, and very prominent orbits. These forms are abundant in pile dwellings. A similar but long-horned type, *Bos macroceros* Dürst, now distributed throughout Africa and Spain, is also, like *B. brachyceros* Owen, of Asiatic origin.

The oldest fossil representatives of the taurine group occur in the later Siwalik beds of northern India. *B. planifrons* and *B. acutifrons* Lydekker.

According to Dürst, *B. planifrons* is the ancestor of *B. primigenius*, whereas *B. acutifrons* and *B. namadicus* Falconer are allied to the *Bibovina* and the zebra. The fossil aurochs, *B. primigenius* Bojanus, the Urus of Julius Caesar, inhabited Europe, but was also distributed throughout Asia and North Africa.

Suborder E. AMBLYPODA Cope.[1]

Extinct, usually large plantigrade ungulates with short, pentadactyl feet and broad terminal phalanges provided with hoofs; second row of carpals alternating with the first. Astragalus very broad and low, articulating with tibia and fibula, the articulating surface for the tibia very slightly concave and smooth, not hollowed out. Dentition usually complete. Cheek teeth brachyodont and lophodont. Brain very small.

The *Amblypoda* comprise some of the largest terrestrial mammals of the Eocene. Their limbs, dentition and entire skeletal structure, besides showing many primitive characters, have also become highly specialised as regards certain features, which are found also, to some extent, among Perissodactyls, Artiodactyls, *Proboscidea* and *Astrapotheria*.

They begin in the Puerco strata (basal Eocene) with rather small and slender forms (*Pantolambda*), which are of a primitive nature as shown by the tritubercular upper molars and the semidigitigrade extremities. The robust and large-sized Coryphodonts having a complete dentition, in which the molars have become lophodont, occur in the Wasatch beds, and in the early Eocene strata in Europe. More highly differentiated are the giant Upper Eocene *Dinoceratidae*, found only in North America. Here the upper incisors are reduced and the upper canines protrude over the lower jaw as great tusks. The lower canine, on the other hand, has become greatly reduced, as is true also of the incisors. The cheek teeth become distinctly lophodont and the premolars molariform.

The extremities are stout, rather high and pentadactyl. The carpals are disposed in slightly alternating rows; a centrale is sometimes present. In the pes the tarsals show a strong, lateral displacement. The low, extremely broad astragalus covers not only the navicular, but, in contrast to the *Proboscidea*, also a large part of the cuboid bone. The navicular rests on the three cuneiform bones. The astragalus lacks a well-defined head, as well as a true trochlea, in which the weakly developed articulating surface of the tibia makes no depression. For this reason only a very slight flexion of the pes is possible. There is an astragalar foramen, besides a facet on the internal side of the astragalus for a so-called tibiale (sesamoid), as is also the case in *Condylarthra*. The calcaneum and the short, stout metatarsals are very like those of the proboscidian foot. There is a third trochanter on the femur in the earliest forms, but this is lacking in the Dinoceratids. The fibula articulates in these forms only with the astragalus.

[1] *Cope, E. D.*, The Amblypoda. Amer. Naturalist, 1884–85.—*Earle, Charles*, Revision of the Species of Coryphodon. Bull. Amer. Mus. Nat. Hist., 1892.—*Gidley, J. W.*, New Paleocene Mammal. Proc. U.S. Nat. Mus., Washington, 1917.—*Hébert, Edmond*, Ann. Sci. Nat., 1856 (Zool.), p. 87.—*Marsh, O. C.*, Amer. Journ. Sci., 1877–81. A Monograph of the extinct order of gigantic mammalia, Dinocerata, Rept. U.S. Geol. Survey, 1884.—*Osborn, H. F.*, Complete Skeleton of Coryphodon and Evolution of the Amblypoda. Bull. Amer. Mus. Nat. Hist., 1898. Skull of Bathyopsis. *Ibid.*, 1913.

The Amblypods have the smallest brain cavity of all ungulates (Fig. 302). The cerebrum is almost entirely smooth and covers neither the olfactory lobes nor the cerebellum.

Osborn derives the *Amblypoda* conjecturally from forms like *Protolambda*, *Ectoconodon* and *Synconodon*, which occur in the Laramie beds of the Cretaceous. This theory rests, however, only upon evidence furnished by isolated tritubercular or tuberculo-sectorial molars. He also unites the bunodont *Periptychidae* and *Pantolambdidae* in the suborder *Taligrada*.

Family 1. **Pantolambdidae** (*Taligrada*) Cope.

Skull resembling that of carnivores, with high sagittal crest. Dentition: $\frac{3.1.4.3.}{3.1.4.3.}$. *Incisors and canines normally developed. Upper premolars consisting of one outer and one inner angulated crescent; upper molars with V-shaped paracone, metacone and protocone, besides two secondary cusps. Lower molars with high V-shaped trigonid and similar talonid, and premolars with only slightly developed talonid. Humerus with an entepicondylar foramen, femur with third trochanter, astragalus flat, with slightly concave articular surface for the tibia, head distinct but very short and with a foramen. Carpus with free centrale. Tail long.*

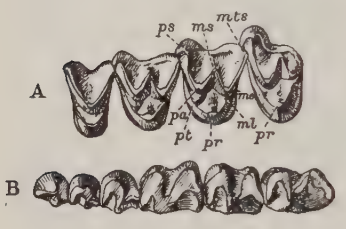


Fig. 298.

Pantolambda cavirictus Cope. Lowest Eocene (Torrejon beds), New Mexico. *A*, Upper P^4 to M^3. *B*, Lower cheek teeth. $^2/_3$. (After Osborn.)

Pantolambda Cope (Figs. 298, 299). Basal Eocene (Torrejon beds) of New Mexico. *P. bathmodon*, *P. cavirictus* Cope.

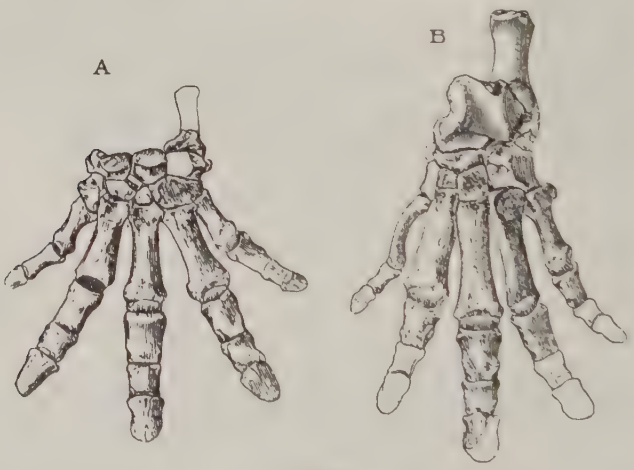


Fig. 299.

Pantolambda bathmodon Cope. Lowest Eocene (Torrejon beds), New Mexico. *A*, Fore-foot. *B*, Hind-foot. $^1/_3$. (After Osborn.)

Family 2. Coryphodontidae Marsh.

Skull elongated, with broad obliquely sloping frontals. Dentition complete. Upper molars with anterior ridge and two outer cusps joined by a V*-shaped ridge*

FIG. 800.

Coryphodon testis Cope. Lower Eocene (Wasatch beds), Wyoming. Skull and lower jaw. 1/6. (After Osborn.)

FIG. 801.

Coryphodon elephantopus Cope. Lower Eocene, New Mexico. Skull, palatal aspect. 1/6. (After Cope.)

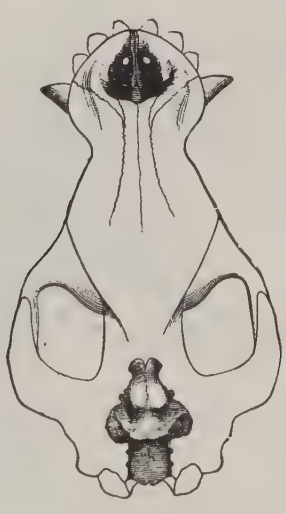


FIG. 802.

Coryphodon hamatus Marsh. Lower Eocene, Wyoming. Outline of skull, upper aspect, with drawing of brain. 1/6. (After Marsh.)

also with one or two unequally developed inner cusps, from which ridges extend to the outer cusps. Lower molar with two V*-shaped ridges, the* V *opening inwardly, and its anterior branch reduced. Premolars simpler than molars. Incisors conical, upper and lower canines pointed and much elongated. Body small in proportion*

to the skull. Humerus without entepicondylar foramen. Femur with third trochanter. Astragalus very low, without head and with slightly concave articular surface for the tibia and fibula.

The *Coryphodontidae* were clumsy animals of considerable size, with digitigrade anterior and posterior extremities. As indicated by their dentition

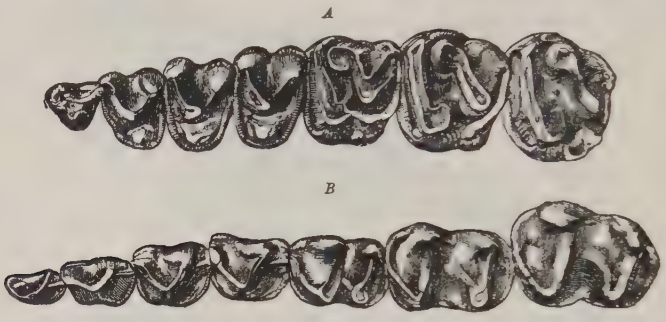


FIG. 303.

Coryphodon hamatus Marsh. Lower Eocene, Wyoming. *A*, Left upper cheek teeth. *B*, Left lower cheek teeth. 1/2. (After Marsh.)

they were of omnivorous habits, and the structure of the feet suggests that they progressed slowly and awkwardly. The skull lacks the peculiar bony horns or bosses on the forehead which are found in the *Dinocerata*, and in lieu of horns they made use of the strong, sharp canines as protective weapons. In general appearance *Coryphodon* was more like a bear than a true ungulate.

FIG. 304.

Coryphodon anax Cope. Lower Eocene (Wasatch beds), Wyoming. Left hind-foot. 1/4. *fb*, Facets on astragalus and calcaneum for fibula; *tb*, tibia. (After Osborn.)

Of the genera *Coryphodon* Owen (*Bathyopsis*, *Bathmodon*, *Metalophodon* Cope) (Figs. 300-304), *Ectacodon* and *Manteodon* Cope, only the first mentioned is well known, and is represented in the Wasatch and Wind River beds of Wyoming and New Mexico by more than a dozen species. Among these, several lines of evolutionary progression can be traced. Several species exhibit analogy to the *Dinoceratidae* in the development of the canines and incisors and also in the structure of the skull. In Europe *C. eocaenus* Owen and *C. oweni* Hébert are found in northern France, Belgium and England.

Family 3. Dinoceratidae Marsh.

Skull with three pairs of processes developed by the frontals, maxillary and nasals. Dental formula: $\frac{0.1.\ 3.\ 3.}{3.1.4\text{-}3.3.}$. *Upper incisors lacking. Upper premolars molariform,*

having two inwardly converging ridges. Lower molars with two transversely oblique ridges. Upper canine very large, descending far below the row of teeth in the lower jaw. Lower incisors and canines small. Condyle of the lower jaw directed back-

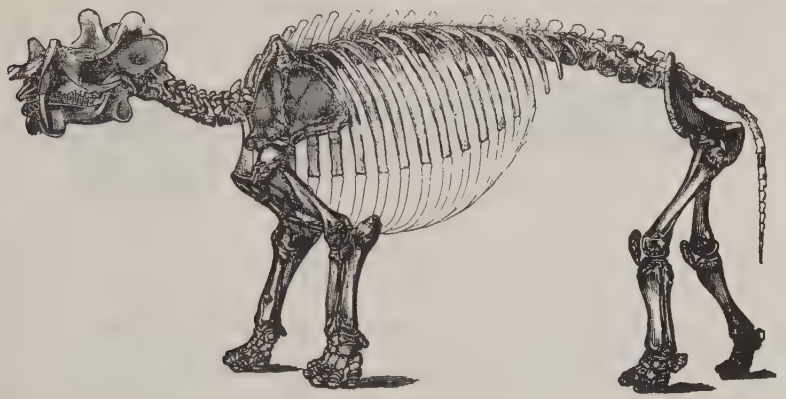


FIG. 305.

Uintatherium mirabile Marsh sp. Middle Eocene (Bridger beds), Wyoming. Skeleton restored by Marsh. $^1/_{13}$.

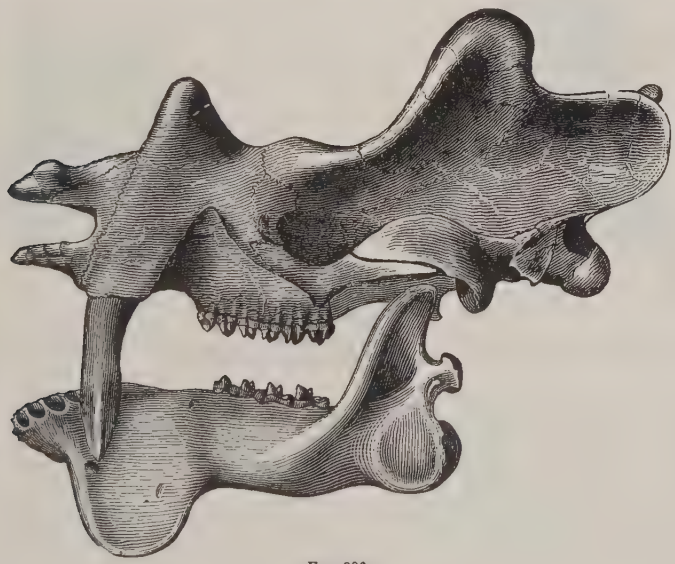


FIG. 306.

Uintatherium mirabile Marsh sp. Middle Eocene (Bridger beds), Wyoming. Skull and lower jaw. $^1/_8$. (After Marsh.)

wardly and only slightly higher than the teeth. Femur without third trochanter. Abundant in the Middle (Bridger beds) and Upper Eocene of Wyoming.

The *Dinoceratidae* comprise some of the most powerful and peculiar of all terrestrial mammals. The largest forms, such as *Loxolophodon* (*Tinoceras*),

reached a height of 2 metres and a length of almost 4 metres. They were, therefore, almost as tall as elephants. Other smaller forms exceeded the hippopotamus and rhinoceros only slightly in height.

Uintatherium Leidy (*Dinoceras* Marsh; *Octotomus* Cope) (Figs. 305-308). The protuberances on the nasals are small and vertical, the spongy bony crests on

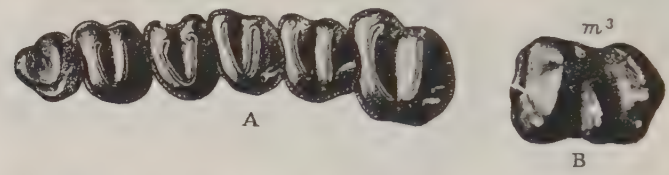


FIG. 307.

Uintatherium mirabile Marsh sp. Middle Eocene (Bridger beds), Wyoming. *A*, Upper cheek teeth. *B*, Last left lower molar. 1/2. (After Marsh.)

the frontals high and rising directly over the condyles of the lower jaw. The powerful, upper canine closes outside a broad, rounded projecting process on the lower jaw. The upper and lower molars and premolars have two inwardly converging transverse ridges. The brain-cavity is very small. The

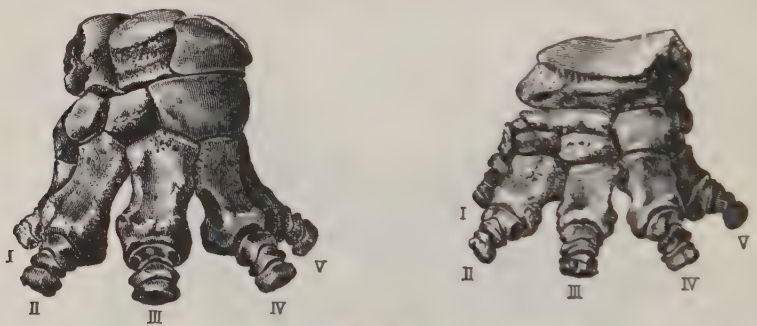


FIG. 308.

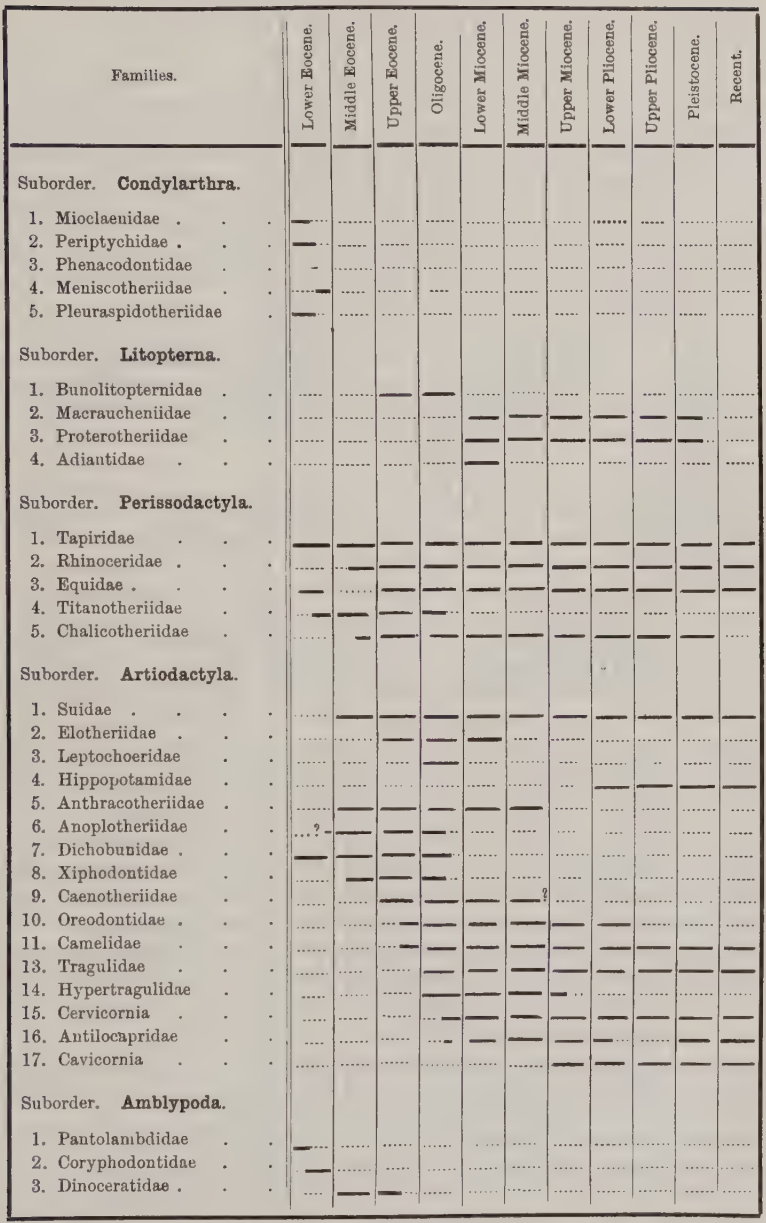
Uintatherium mirabile Marsh sp. Middle Eocene (Bridger beds), Wyoming. *A*, Left fore-foot. *B*, Left hind-foot. 1/5. *as*, astragalus. (After Marsh.)

pelvis and extremities, on account of becoming adapted to serve similar functions, are very like those of the *Proboscidea*. The hind-limbs are somewhat longer than the fore-limbs. The feet are pentadactyl. Several species are known from the Middle and Upper Eocene of Wyoming.

Loxolophodon Cope (*Tinoceras* Marsh). Very similar to the preceding, but with larger nasal protuberances, directed obliquely forward. The frontal crests extend to a point behind the condyles of the lower jaw. Same horizon and locality.

Eobasileus Cope. From uppermost Bridger Beds, Wyoming.

Geological Distribution of the Ungulata.



Order VIII. NOTOUNGULATA Santiago Roth.[1]

Extinct herbivores, restricted to South America. Feet varying between the plantigrade and semidigitigrade forms, and having from three to five toes. Skull flat and low, with broad frontals and occiput. Zygomatic arch strong, extended posteriorly to the supraoccipital crest. Nasals broad, nostrils usually at anterior extremity. Orbits large and only partially separated from the temporal vacuity. The mastoid region usually much expanded. Mandible high and massive, as a rule with strong symphysis. Dentition ordinarily complete, usually without diastema, frequently having the upper incisors enlarged and the remaining incisors, as well as the canines, premolars and molars passing from one form of tooth to the next by gradual transitions. Teeth brachyodont to hypsodont, prismatic. Upper molars with an external ridge (ectoloph), or a long, oblique protoloph, and a short, straight metaloph. Lower molars comprising two semilunar ridges of unequal size and two inner pillars. Carpals alternating, free, centrale lacking. Astragalus with a narrow trochlea, which is often furrowed, and has also a convex articulation for the navicular. Fibula always articulating with the calcaneum. Terminal phalanges developed as small blunt claws, as hoofs, or as strong fissured claws.

The *Notoungulata* exhibit in their external appearance many characters of the *Hyracoidea* and those of rodents. The resemblance is seen principally in the breadth and flatness of the cranial roof, in the powerful development of the jugal arch, in the breadth of the occiput, in the position and size of the orbits, in the height of the mandible, and in the enlargement of the foremost incisors. The individual bones, too, are not unlike those of the *Hyracidae* and some rodents. Close observation, however, reveals several fundamental differences. For instance, the incisors are not compressed laterally as in rodents, but in an antero-posterior direction. The reduction in the number of teeth, too, is only slight in this group. The *Notoungulata* are distinguished from the *Hyracoidea* by the alternating arrangement of carpals, by the articulation of the fibula with the calcaneum, by the simple lateral articulation of the malleolus of the tibia with the astragalus, and above all by the dentition. The teeth of the *Hyracoidea* are first bunodont, and later the two ridges of the upper molars and the two semilunar ridges of the lower molars become equal in size, whereas in the *Notoungulata* the metaloph of the upper and the anterior semilunar ridge of the lower molars are always much smaller than the protoloph and the posterior semilunar ridge.

The molars of the *Notoungulata* (Fig. 309) are formed on the tritubercular or tuberculo-sectorial type. The two outer cusps of the upper molars are very close to the outer edge—ectoloph, the anterior inner cusp—protocone—

[1] *Ameghino, Florentino*, Contribuciónes al conocimiento de los mamiferos de la Republica Argentina. Buenos Aires, 1889.—Mammifères crétacés de l'Argentine. Bolet. del Instit. Geografico Argentino, vol. xviii., 1897.—Recherches de morphologie phylogénétique sur les molaires supérieurs des ongulés. Anal. Mus. Nac. Buenos Aires, vol. ix., 1904.—Notices sur des ongulés nouveaux des terrains crétacés de Patagonie. Bol. Acad. Nat. de Cienc. de Cordoba, 1901, 1902.—*Burmeister, H.*, Description physique de la Republica Argentina, 1879, vol. iii.—*Gaudry, A.*, Dentition de quelques mammifères. Mém. Soc. Géol. de France, Paleont., 1906.—Fossiles de Patagonie. Annal. de Paléontologie, 1906, 1908. *Gregory, W. K.*, The orders of mammals. Bull. Amer. Mus. Nat. Hist., New York, 1910, vol. xxvii.—*Lydekker, R.*, Palaeontologia Argentina II. Anal. Mus. de la Plata, 1893.—*Roth, Santiago.*, Los ungulados suramericanos. Anal. Mus. de la Plata. Paleontologia, 1903.—*Scott, W. B.*, Classification of the Notoungulata. Science, vol. xxi., 1905.

becomes a long, oblique protoloph, and the hypocone a short, straight metaloph. Frequently also crests or crochet-like spurs are formed on these molars, and a parastyle appears on the front surface, so that these teeth display a certain similarity to the upper molars of the rhinoceros. On the posterior surface still another ridge may develop from an extra cusp. The molars of primitive forms are much broader than long. The lower molars consist of two outer semilunar ridges, of which the anterior one is much shorter than the posterior, and is formed from two more or less compressed inner cusps. The foremost of these is joined inwardly with the posterior portion of the first semilunar ridge, whereas the hinder one lies opposite the second semilunar ridge, frequently remaining entirely isolated. These molars have a general resemblance to those of the *Litopterna*, but they pass through no well-defined bunodont stage in their development. The conformation of the

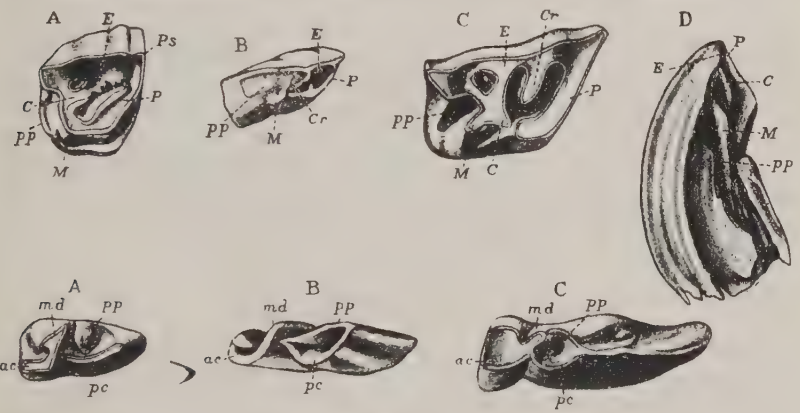


Fig. 309.

Upper and lower molars of Notoungulata, showing grinding surface. Upper molars: *A*, *Pleurostylodon*. *B*, *Protypotherium*, 2/1. *C*, *Rhynchippus*. *D*, *Rhynchippus*. M^3 from behind. Lower molars: *A*, *Pleurostylodon*. *B*, *Protypotherium*, 2/1. *C*, *Morphippus*. *C*, crochet; *Cr*, crest; *E*, ectoloph; *M*, metaloph; *P*, protoloph; *Ps*, parastyle; *ac*, anterior crescent; *md*, metaconid; *pc*, posterior crescent; *pp*, posterior pillar.

incisors, canines and premolars gradually leads up to the molariform tooth. Often one or two pairs of incisors are greatly enlarged, or, together with the canines, disappear entirely, or again these latter may develop into tusk-like eye-teeth, in which case one to three premolars are lost. The teeth are originally brachyodont, later becoming hypsodont, and in the final stage they become prismatic and lose their roots entirely (Fig. 310), although even in this case the premolars are considerably lower than the molars.

As indicated by Santiago Roth, the chief distinguishing characteristic of the *Notoungulata* consists in the broadening and swelling up of the mastoid region of the skull, and the joining of this cavity, frequently filled out with spongy, bony tissue, with the tympanic bulla. Even though this distinction is always found among the older forms, yet there are many marked stages in the development of the swelling of the mastoid region, so that there can be no good reason for excluding the *Astrapotherioidea* from the *Notoungulata* because they lack this characteristic.

The bones of the extremities show considerable variation and modification

correlated with the size of body. On the whole, however, they are more nearly comparable with those of carnivores and rodents than with those of true ungulates. The long tibia of small forms is slender, the humerus has an entepicondylar foramen, and the femur a third trochanter. The ulna is very massive and is not fused with the radius. These are frequently crossed.

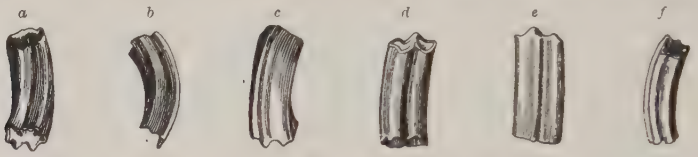


FIG. 310.

Protypotherium australe Ameghino. Upper molar, from inside (*a*), behind (*b*), and outside (*c*). Lower molar, from inside (*d*), outside (*e*), and behind (*f*). 1/1.

All of the carpals are free and alternately arranged. The astragalus always has a convex nearly hemispherical navicular facet; and the fibula, usually not fused with the tibia, always articulates with the calcaneum. The number of metapodials varies between three and five; the median keel of their distal articulation is always restricted to the posterior surface. The terminal phalanges are at times claw-like, although slightly flattened in front, or in other cases broad hoofs, or hooked, deeply fissured claws.

The *Notoungulata* are divided into five suborders as follows: *Typotheria*, *Toxodontia*, *Entelonychia*, *Astrapotherioidea* and *Pyrotheria*.

Suborder A. TYPOTHERIA Zittel.[1]

Extinct plantigrade or digitigrade herbivores usually with four-toed manus and pes. Dentition, as a rule, is complete, the inner, upper incisors enlarged, the outer incisors and canines often reduced, or all the teeth graduating one into another and in a compact row. Upper molars are lophodont, lower ones selenolophodont. In the beginning these were brachyodont and rooted, later they become hypsodont, prismatic and without roots. Clavicle often present. Carpals alternating, centrale lacking. Humerus with entepicondylar foramen. Femur with third trochanter.

The *Typotheria* are restricted to the Tertiary and Pleistocene of South America. They are very closely related to the *Toxodontia*, and resemble in external appearance many rodents and the *Hyracoidea*, though this resemblance depends merely on convergence and not on true relationship.

The skull is like that of rodents in that it is elongated and has a straight transverse suture separating the frontals from the parietals. The forwardly directed nostrils are bounded on the side by the high premaxillary bones, and above by the long nasals reaching to the extremity of the rostrum. The parietals have a small sagittal crest. The zygomatic arch, which is very strongly developed posteriorly, is very high, and the wide orbits are frequently bounded posteriorly by a processus postorbitalis of the frontals. The infra-orbital foramen lies in front of the zygomatic arch. The broad occiput has a supraoccipital crest and a long paroccipital process. The broadening and

[1] *Gervais, P.*, Remarques sur le Typotherium. Zool. et Paléont. Générales, vol. i., 1867-69.—*Sinclair, W. J.*, Report of the Princeton University Expedition to Patagonia, vol. vi., part I. 1909.

inflation of the squamoso-mastoid region in this group attains its highest stage among the *Notoungulata* in *Pachyrucos*, but the character is by no means developed to an equal degree among different genera. This capsule, at times hollow and at times filled with a cellular osseous tissue, is connected with the tympanic bulla, and encloses the broad, upwardly directed auditory meatus. The palate often extends far behind the last molars. The high mandible forms a strong symphysis, and is very like that of *Hyrax* in that it has a broad, ascending ramus and a short coronoid process.

The dentition is ordinarily complete with $\frac{3.1.4.3.}{3.1.4.3.}$ teeth in compact rows; a wide diastema is sometimes formed by the disappearance of the outer incisors, the canines, and of one or two premolars. In the older forms all the teeth are brachyodont; in later forms this applies only to the milk-teeth. The lower incisors often have a deep indent in the middle. The upper I^1 and the lower I_1 and I_2 become larger and longer and more rodent-like, although they are antero-posteriorly compressed rather than transversely. The other incisors, the canines and premolars become very gradually molariform, or else the incisors and canines either degenerate into mere pegs or are lacking entirely. The premolars are usually simpler than the molars, since their posterior moiety usually remains smaller than the anterior one. The upper premolars and molars become bent and inwardly directed prismatic teeth, while those of the lower jaw are outwardly directed. The upper molars consist of an ectoloph, which has a projecting ridge, an oblique protoloph, a somewhat shorter metaloph, a crest and a posterior pillar. The lower molars have two outer crescents and two strongly compressed inner pillars, which at times fuse to form a well-defined ridge. The lower third molar is always much larger than the second. The molars of the *Typotheria* are distinguished from those of the *Toxodontia* by the posterior and anterior moieties being of nearly equal size, and by the rapid disappearance of the valleys in the wearing down of the teeth. The upper molars are further distinguished by the noticeable elongation of the grinding surface and by the secondary spurs. The teeth are often provided with a thin layer of cement.

FIG. 311.

Typotherium cristatum Serres. *a*, Acromial process; *c*, coracoid process. (After Gervais.)

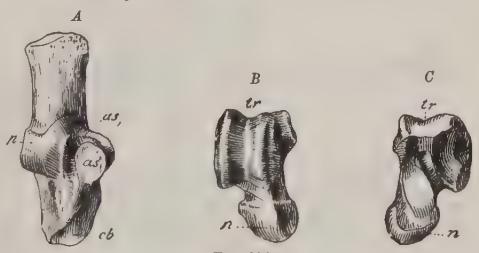


FIG. 312.

Protypotherium. *A*, Calcaneum, anterior aspect. *as*, Facet for astragalus; *cb*, for cuboid; *p*, for fibula. *B*, *C*, Astragalus, anterior and posterior aspects. *n*, Facet for navicular; *tr*, trochlea for tibia.

The dorsal vertebrae are fifteen in number, the lumbars seven, and the sacrals five. This is true at least for the *Typotheria* of the Miocene of Santa Cruz. The tail seems to have been long in most cases. The scapula (Fig. 311) has an acromial and coracoid process, and articulates, no doubt, with a well-

developed clavicle. The humerus has an entepicondylar foramen. Ulna and radius are not fused and are but slightly bent. The arrangement of carpals is always alternating. The centrale is fused with the scaphoid. There are four metacarpals, the pollux is entirely atrophied, and the fifth finger somewhat reduced. In the case of *Typotherium*, however, the second to fifth digits are almost of the same length, and the first is short, but having phalanges. The terminal phalanges are pointed, but expanded on the under side into a triangular flat surface, or hoof-like and cleft in front.

The femur has a fairly large projecting third trochanter. The tibia and fibula are sometimes free, sometimes fused at the extremities. The calcaneum (Fig. 312 A) has a long, thick tuberosity, a broad, convex facet for the articulation of the fibula, and a large articular surface for the cuboid, whereas the sustentaculum projects only slightly. The astragalus (Fig. 312 B, C) is distinguished by the narrow, not very deeply-grooved trochlea, and the well-rounded, stalked head. Of the four metatarsals those laterally placed are often somewhat more slender than the others. On the whole, the skeleton agrees closely with the original carnivore type, exhibiting, however, many peculiar rodent-like specialisations.

Family 1. **Notopithecidae** Ameghino.

$\frac{3.1.4.3.}{3.1.4.3.}$ *in compact rows, brachyodont and with roots. Incisors, canines and premolars gradually intergrading.* I^1 *to* P^1 *trenchant, the lower incisors and canines chisel-shaped,* P^2 *to* P^4 *triangular,* M^1 *to* M^2 *rhombic,* M^3 *rounded triangular with ectoloph, two dissimilar transverse ridges confluent on the inner side and posteriorly with a basal cingulum, together with a small mesially placed spur. Lower molars with two outer crescents and two inner cusps, of which the first is fused with the first crescent and the second is free. Mandible rather weak.*

FIG. 313.

Adpithecus serus Ameghino. Upper Eocene (Notostylops beds), Patagonia. *A*, Upper and lower series of teeth, 1/1. *B*, Upper and lower molar, 2/1. *C*, Upper jaw, 1/2. *D*, Lower jaw, 1/2.

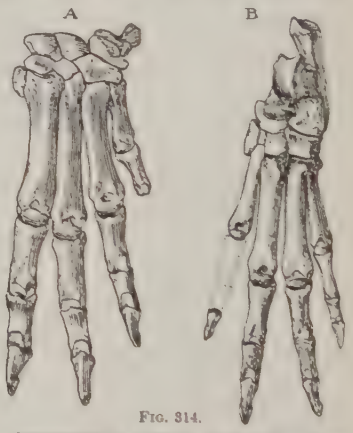


FIG. 314.

Protypotherium australe Ameghino. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Fore foot, 3/4. *B*, Hind foot, 1/2. (After Sinclair.)

The following genera, of about the size of a hare and restricted to the Eocene (Notostylops beds) and the Oligocene of Patagonia, are forerunners of the two families immediately to be considered.

Notopithecus, *Adpithecus* (Fig. 313), *Transpithecus*, *Infrapithecus*, etc., Ameghino. Notostylops beds. *Guilelmoscottia* Ameghino. Astraponotus beds.

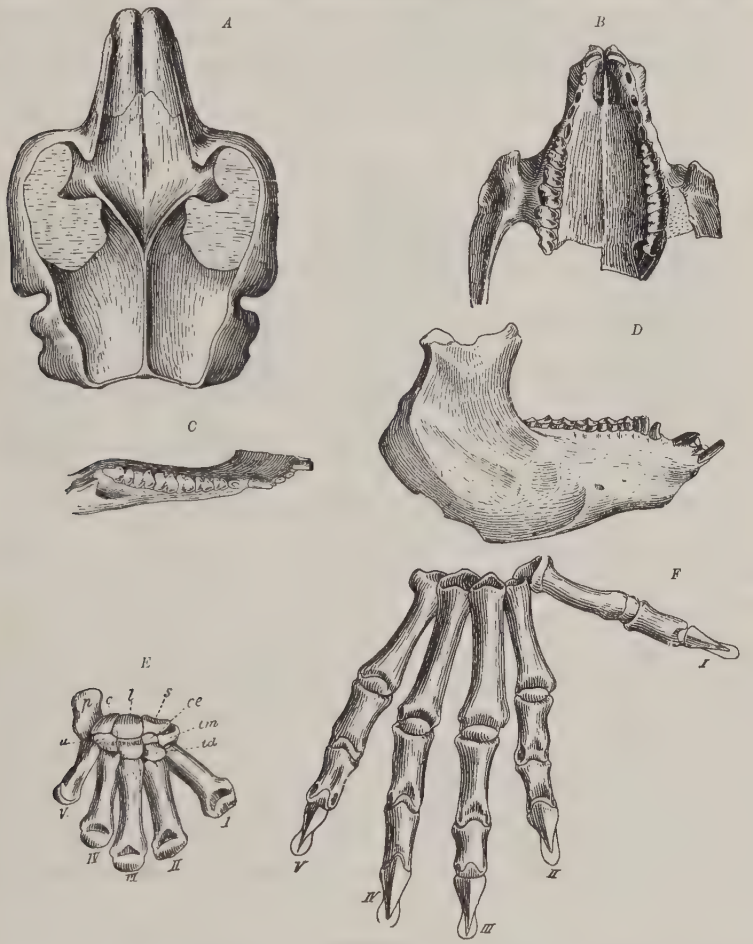


FIG. 315.

Interatherium robustum Ameghino. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Skull, upper aspect. *B*, Palate, etc. *C*, *Interatherium extensum* Ameghino, Same formation. Right ramus of lower jaw, upper aspect. *D*, Same, outer aspect, $^3/_4$. *E*, Right fore foot. *F*, Right hind foot. $^1/_1$. (After Ameghino.)

Family 2. Interatheriidae Ameghino.

$\frac{3.1.4.3.}{3.1.4.3.}$ *I_1 is rooted, all the other incisors prismatic. P_3 and P_4 simple. Upper molar with inner valley. Mastoid filled with cellular tissue, zygomatic arch*

beginning far behind the maxilla. Mandible high. Jugal with a downwardly directed process. Tibia and fibula free. Outer toes reduced.

Protypotherium (*Patriarchus*) Ameghino (Figs. 309B, 310, 312, 314). Jugal with small process. Teeth gradually transitional from one form to the other. Miocene of Santa Cruz. *P. australe*, *P. attenuatum* Ameghino.

Interatherium (*Icochilus*) Ameghino (Fig. 315). Lateral incisors and canines reduced. Jugal with well-developed process. Humerus with indistinct foramen. Miocene of Santa Cruz. *I. robustum*, *I. extensum* Ameghino.

Cochilius Ameghino. Miocene. Colpodon beds.

Plagiarthrus Ameghino. Teeth rooted in old age. Pyrotherium beds.

Family 3. **Hegetotheriidae** Ameghino.

I_1 is enlarged. P_3 and P_4 are molariform. Upper molars are convex on the inner side, outside they are smooth. Mastoid is hollow, malar adjacent to maxilla. Tibia and fibula fused. Outer toes unequally reduced.

Hegetotherium (*Selatherium*) Ameghino. $\frac{3.1.4.3.}{3.1.4.3.}$ Posterior incisor and canine somewhat reduced. Terminal phalanges flattened. Tail long. About the size of a fox. Miocene. Colpodon and Santa Cruz beds. *H. mirabile* Ameghino.

Archaeopilus, *Prohegetotherium* Ameghino. Lower Miocene. Pyrotherium beds.

Prosotherium Ameghino. $\frac{1.0.4.3.}{2.0.4.3.}$ Pyrotherium beds.

Eohegetotherium Ameghino. Teeth with roots. Oligocene. Astraponotus beds.

Pachyrucos Ameghino (*Paedotherium* Burmeister). $\frac{1.0.3.3.}{2.0.3.3.}$ Mastoid region extremely inflated. Terminal phalanges hoof-like. Tail short. Miocene. Santa Cruz. *P. moyani* Ameghino. About the size of a rabbit. Occurs in the Colpodon beds and also in the Pliocene and Pleistocene. Monte Hermoso. *P. typicus* Ameghino.

Eopachyrucos, *Pseudopachyrucos* Ameghino. Astraponotus beds. *Propachyrucos* Amegh. Pyrotherium beds.

Argyrohyrax Ameghino. $\frac{3.1.4.3.}{\quad\quad}$ The last incisor, the canine and P^1 and P^2 gradually leading from one form to the next. P^3 and P^4 are molariform. Pyrotherium beds.

Family 4. **Typotheriidae** Ameghino.

$\frac{1.0.2.3.}{2.0.1.3.}$ *I^1 broad, bent and open at the base, with enamel on the front surface. I_2 small. Behind the incisors there is a long diastema. Upper premolars with two, molars with three ridges. Anterior moiety of the lower molars much shorter than the posterior. All the molars are prismatic and partially covered with cement. Carpals alternating. Manus with slender pollex. Fibula not articulating with the calcaneum.*

Typotherium Bravard (Figs. 311, 316). Attaining nearly the size of a pig. Lower Pleistocene of Argentina.

Trachytypotherium Ameghino. Pliocene.

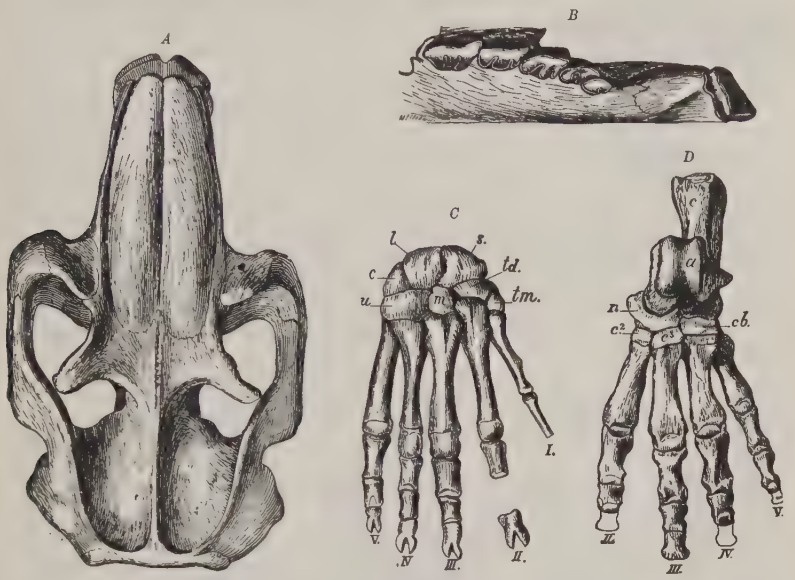


FIG. 316.

Typotherium cristatum Serres. Pampas Formation, Buenos Aires, Argentina. *A*, Skull, upper aspect. *B*, Upper jaw, palatal aspect. *C*, Right fore foot. *D*, Left hind foot. 1/4. (After Gervais.)

Eutrachytherus and *Proëdrium* Ameghino. Dentition: $\frac{3.1.4.3.}{2.1.4.3.}$. Pyrotherium beds of Patagonia. Systematic position somewhat doubtful.

Family 5. **Archaeopithecidae** (*Henricosborniidae*, *Pantostylopidae*) Ameghino.

Premolars simpler than molars. Upper premolars and lower third molars are triangular, lower first and second molars are oblong, much broader than long. Ectoloph with parastyle, often also with mesostyle and metastyle. Protoloph oblique and longer than metaloph. Both ridges often joined on the inner side. Crista and crochet sometimes also present. The posterior crescent of the lower premolars is smaller than the anterior, in the molars the posterior crescent is the larger of the two. Premolars with only one central cusp, situated at the junction of the two crescents; molars with a second central cusp, which is near the posterior end of the second crescent. All teeth are brachyodont. Lower jaw (known in Selenoconus) rather low. About the size of a rabbit.

Possibly the forerunners of the *Archaeohyracidae*, but not related to the *Primates* or to the *Hyracidae*. Restricted to the Eocene, Notostylops beds of Patagonia. *Henricosbornia*, *Othnielmarshia*, *Archaeopithecus*, *Pantostylops*, etc., Ameghino.

The *Acoelodidae* are distinguished from the *Archaeopithecidae* only by their greater size, being about the size of a fox, and by the more oblique trapezoidal outline of the upper molars.

FIG. 317.

Oldfieldthomasia sp. Upper Eocene (Notostylops beds), Patagonia. *A*, Upper cheek teeth. *B*, Lower second and third molars. 1/1.

Acoelodus, Oldfieldthomasia (Fig. 317), *Eohyrax, Acoelohyrax*, etc., Ameghino. Eocene. Notostylops beds of Patagonia.

Family 6. **Archaeohyracidae** Ameghino.

Skull similar to that of Hegetotherium, having, however, weaker jugals and a more slender lower jaw. Dentition: $\frac{3.1.\ 4.\ 3.}{3.1.4\text{-}3.3.}$ *Superior incisors fairly large, the lower incisors and canines peg-like, the lower premolars molariform. All of the upper teeth gradually intergrade from one form to the next; thus the molars have an oblique, triangular outline and have a parastyle like the premolars. All of the teeth are prismatic. M_3 with large third lobe.*

These are probably the ancestors of *Typotherium*. Lower Miocene (Pyrotherium beds) and Oligocene (Astraponotus beds). *Archaeohyrax* Ameghino.

Suborder B. TOXODONTIA Owen.[1]

Extinct, digitigrade or semiplantigrade herbivores with three-toed extremities. Dentition usually complete. Canines always weak, often lacking entirely. Molars curved and lophodont. Clavicles wanting. Carpals alternating. Astragalus with rather convex, slightly furrowed articulation for the tibia, distally foreshortened, articulating only with the navicular. Calcaneum stout with a large articular surface for the fibula. Humerus without entepicondylar foramen.

The *Toxodontia* are medium-sized and large herbivores, restricted to South America, beginning in the Oligocene (?) of Patagonia and becoming extinct in the Pleistocene of Argentina and Brazil.

The skull is moderately high, its roof frequently being almost flat, and sloping from the protruding rostrum to the occiput. The muzzle is slender and rather long. The frontals are large, the parietals develop a weak sagittal crest. The high and broad occiput is abruptly truncated downward, the squamoso-mastoid region is not greatly inflated, and the exterior auditory meatus opens obliquely upward. The condyles are rather prominent. The zygomatic arch is unusually high but not very thick. Below the orbit, which is open posteriorly, the arch curves downwardly and consists principally of a process of the squamosal. The premaxillaries are elongated and high. The lachrymal is small. The arched palate extends beyond the hindmost molars so that the inner choanae are pushed far backward. The anterior palatal vacuities are entirely surrounded by the premaxillaries. Lower jaw with

[1] *Burmeister, H.*, Anales del Museo de Buenos Aires, vol. i., 1867, and vol. iii.—*Cope, E. D.*, On Toxodon. Proc. Amer. Philos. Soc., 1881. —*Lydekker, R.*, Anales del Museo de La Plata. Paleontologia Argentina, 1890. —*Owen, R.*, (Toxodon) in the Zoology of H.M.S. *Beagle*, 1840.—Description of some species of Nesodon. Philos. Trans., 1853. *Roth, Santiago*, Catálogo de los mamíferos fósiles en el Museo de La Plata. Orden Toxodontia, 1898.

very strong symphysis, broad coronoid process and high, transverse condyle. The dentition is frequently complete, highly specialised, and teeth often in compact series. The incisors are often spade-like, entirely or partially covered with enamel, and all or in part with closed roots. In some forms they may be very much elongated, rodent-like, open below and having enamel front and back or only on the front surface. I^2 and I_3 are very strongly developed. All of the upper teeth from the third incisor on, and all of the lower teeth from the canine on, gradually intergrade (Fig. 318). Of the four premolars, the two anterior ones may be reduced and the two posterior ones become molariform. The upper molars have an oblique quadrangular or triangular outline, and usually a parastyle. They are made up of an ectoloph and two unequally developed ridges, between which there is a deep transverse valley where there are one or two small crests. On the posterior surface often another ridge is formed. By continued grinding, all of these prominences are worn down until the valleys appear as islands, and these later also become

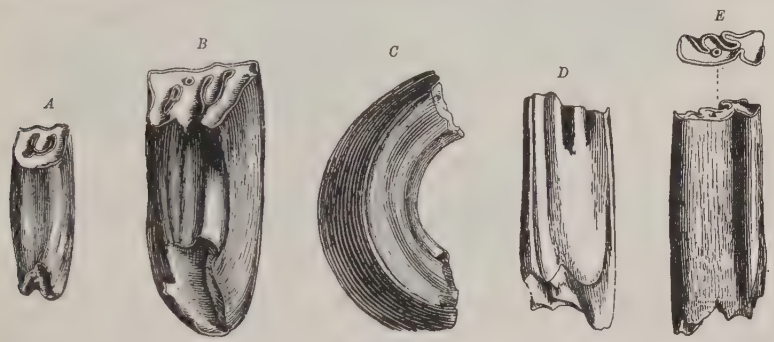


FIG. 318.

Adinotherium sp. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Upper premolar from inside. *B*, *C*, Upper molar from inside and from behind. *D*, Lower molar from outside. *E*, Lower molar from inside and above. $^2/_3$.

worn down either completely or in part. In the primitive forms the crowns are entirely covered by enamel; among higher types the cheek teeth become prismatic, the roots disappear, and enamel is restricted to the outer and anterior sides or to the outer and inner sides. Often there is a cement covering which surrounds the tooth either entirely or in part. The lower cheek teeth consist of a short anterior and a much longer posterior crescent, besides two inner pillars, the anterior of which fuses with the hinder end of the first crescent, and the base of the posterior pillar fuses with the anterior end of the second crescent. The prominences of the inner side are worn down by grinding to form a sort of endoloph. The original valleys of these teeth also become enamel islands. The upper incisors and molars are very strongly curved inwardly, the lower ones forwardly. The third molar is elongated in both jaws. The posterior milk-teeth resemble, on the whole, the molars, but always have short, separate roots.

The skeleton of the *Toxodontia* is very similar to that of the Typotheres and combines many primitive characteristics with high specialisation. The large scapula is similar to that of the rhinoceros, only having a rudimentary acromion, which indicates that no clavicle is present. The short, strong

humerus has a low, simple trochlea, but no entepicondylar foramen. The robust ulna with long, well-developed olecranon, and the short, somewhat slighter radius, are crossed; otherwise they are not unlike those of the rhinoceros, and the same is also true of the pelvic girdle. The carpals are alternating, the metacarpals short and thick (Fig. 319). The short femur has a weak third trochanter; its first trochanter is strongly projecting outward.

Fig. 319.

Toxodon paranensis Laurillard. Pliocene, Argentina. Fore foot. *c*, cuboid; *l*, lunar; *m*, magnum; *p*, pisiform; *sc*, scaphoid; *td*, trapezoid; *u*, unciform.

Fig. 320.

Adinotherium sp. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Calcaneum, anterior aspect. *B*, *C*, Astragalus, anterior and posterior aspects. 2/3.

The massive fibula may become fused with the tibia. The former articulates inwardly with the stout calcaneum (Fig. 320 A). The astragalus (Fig. 320 B) has a faintly arched and moderately deep trochlea, and its short, inwardly directed neck has a weakly convex articular surface for the navicular. The short, stout metatarsals and metacarpals have weak, obtuse keels. The end phalanges form flattened hoofs. Manus and pes only have three digits each.

Family 1. **Notohippidae** Ameghino.

$\frac{3.1.4.3.}{3.1.4.3.}$ *All of the teeth compactly set, hypsodont, with roots in old age, and intergrading gradually from the first incisor to the last molar; in some cases the lower incisors and canine may be chisel-shaped or spade-like, but never enlarged. Cranial roof flat, nares terminal. Astragalus with a rather long neck.*

The specialisation of the incisors and canines is not as strongly marked in this family as in the *Nesodontidae*. The premolars and molars are still covered with enamel on all surfaces. The posterior margin of the upper molars forms a third ridge. The inflation of the mastoid region is very slight in these forms.

Notohippus Ameghino. Miocene of Patagonia.

Rhynchippus Ameghino (Fig. 309 C, D). Incisors and canines chisel-shaped.

Morphippus Ameghino (Fig. 309 C). Incisors and canines spade-like, the incisor being like that of a horse.

Coresodon Ameghino. Limited to the Lower Miocene; Pyrotherium beds.

Argyrohippus Ameghino. Teeth with thick cement covering. *Stylhippus*, *Perhippidium* Ameghino. Miocene; Colpodon beds.

Eomorphippus and *Interhippus* Ameghino. Oligocene; Astraponotus beds.

Family 2. **Nesodontidae** Murray.

$\frac{3.1.4\ 3.}{3.1.4.3.}$ *Teeth usually in a compact row.* I^1 *and* I^2 *enlarged,* I^1 *chisel-shaped, with enamel covering only on the anterior surface,* I^2 *triangular, without enamel on*

FIG. 321.

Nesodon imbricatus Owen. Upper Miocene (Santa Cruz beds), Patagonia. Skull and lower jaw. 1/6.

posterior surface. I^3, *C and* P^1 *small, gradually merging into and becoming similar to the other premolars, and separated from one another by short vacant spaces. Lower incisors chisel-shaped,* I_3 *enlarged. Upper premolars and molars increasing in size posteriorly, prismatic, having enamel only on the outer and front surface, strongly bent inwards, the inner side of the two transverse ridges becoming fused as they are worn down, and surrounding an island. Lower molars with enamel only on the outer and inner surfaces and very strongly compressed. Teeth developing roots only in old age, and then only partially.*

Nesodon Owen (*Gronotherium*, *Phobereotherium* Ameghino) (Figs. 321-323). Larger than a tapir and one of the most abundant mammals in the Miocene of Santa Cruz. Patagonia. *N. imbricatus* Owen.

Stenostephanus Ameghino. Imperfectly known. Miocene and Pliocene.

Trigodon Ameghino. With horn-like excrescence on the forehead. Pleistocene of Monte Hermoso.

Adinotherium Ameghino (Figs. 318, 320). Upper I^3, C and P^1 very small. Miocene; Colpodon beds and Santa Cruz beds. *A.* (*Nesodon*) *ovinum* Owen.

Pronesodon, *Proadinotherium* Ameghino. Miocene; Pyrotherium and Colpodon beds of Patagonia.

Acrotherium Ameghino. Similar to *Adinotherium*. Miocene of Santa Cruz.

Family 3. Toxodontidae Ameghino.

Cheek teeth very strongly compressed, narrower and (because of the fusion of processes on the inner surface) simpler than those of the Nesodontidae. Upper molars

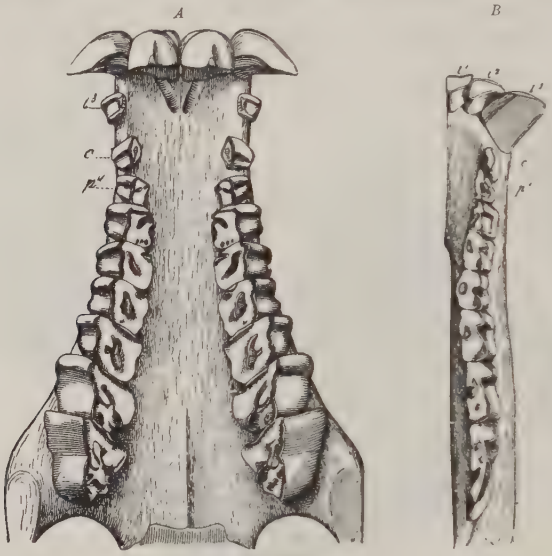


FIG. 322.

Nesodon imbricatus Owen. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Palate of adult individual with complete dentition. *B*, Right lower dentition. 1/3. (After Ameghino.)

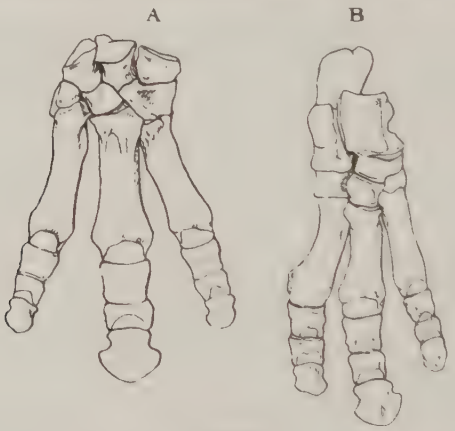


FIG. 323.

Nesodon imbricatus Owen. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Fore foot. *B*, Hind foot. 1/5. (After Sinclair.)

apparently consisting only of ectoloph and protoloph. Dentition often with a diastema, due to the degeneration of the canine and premolars. All of the teeth prismatic and

without roots, covered with enamel on all sides, but the outer surface interrupted by bands in which the enamel is lacking. Astragalus with flattened trochlea.

Toxodontherium Ameghino. (*Haplodontherium* Ameghino.) $\frac{3.1.3.3.}{3.1.3.3.}$. Upper premolars and molars still rather broad. Pampas formation, Argentina.

Xotodon Ameghino. $\frac{2.1\ 4.3.}{3.1.4.3.}$. Both occur in the Pliocene and Pleistocene of Argentina.

Toxodon Owen (Fig. 324). $\frac{2.0.3.3.}{3.1.4.3.}$. The largest member of the suborder,

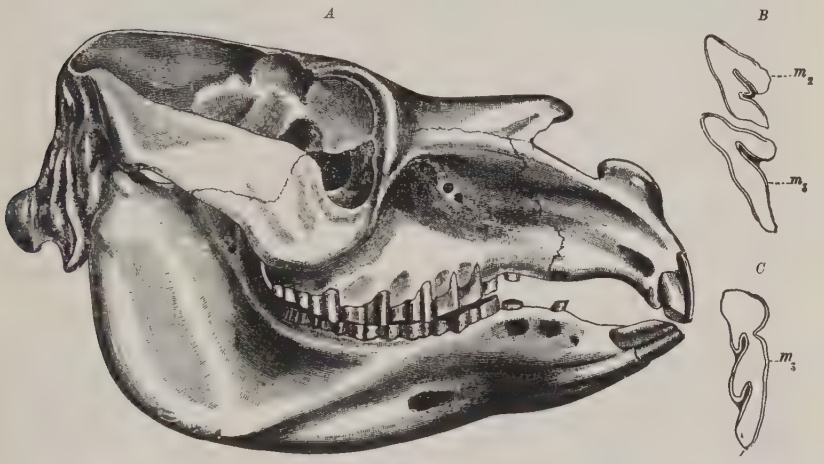


FIG. 324.

Toxodon burmeisteri Giebel. Pleistocene (Pampas Formation), Lujan, Argentina. *A*, Skull and lower jaw. 1/7. *B*, Upper first and second molars, grinding surface. *C*, Lower third molar, grinding surface. (After Burmeister.)

exceeding the rhinoceros in its dimensions. Nasals short, nostrils rather remote. Pliocene and Pleistocene (Pampas formation) of Argentina and Bolivia. *T. platensis* Owen.

Suborder C. ENTELONYCHIA Ameghino.[1]

(*Ancylopoda, Tillodontia* Ameghino.)

Extinct, plantigrade or semidigitigrade herbivores with complete, seldom reduced dentition. Incisors, canines and premolars either passing into one another, or in both the upper and lower jaws one incisor strongly developed. Lower canine sometimes resembling an eye-tooth. Premolars and molars lophodont, varying from brachyodont to hypsodont type and always with roots. Premolars simpler than the

[1] *Ameghino, Florentino,* Énumération synoptique des mammifères fossiles de Patagonie. Buenos Aires, 1894.—Sur les ongulés fossiles de l'Argentine. Revista de Jardin zoologico Buenos Ayres, 1894.—Notices préliminaires sur des ongulés des terrains crétacés. Boletin Acad. Nacional de Cienc. de Cordoba, vol. xvi., 1901.—*Flower, W. H.*, Homalodontotherium. Philos. Trans., 1874.

molars. Upper molars almost always broader than long, consisting of an ectoloph and two unequal transverse ridges, and always with crochet and often also with crests. Lower molars with a very short anterior crescent, an elongated posterior one, and two inner cusps, of which the first is considerably extended transversely. Carpals alternating. Calcaneum long, with a small, usually transverse facet for articulation with the fibula. Astragalus with foramen above the flat tibial facet, the upper margin of which is deeply excavated. Terminal phalanges frequently developed as stout, curved claws, or as broad hoofs, always fissured in front. Manus and pes pentadactyl.

The *Entelonychia* include medium-sized to large herbivores, and are restricted to the Tertiary of Patagonia. They possess certain characters, such as form and retractability of the terminal phalanges, in common with the so-called *Ancylopoda* (now *Chalicotheriidae*) of Cope. On the other hand, the dentition most decidedly indicates close relationship with the *Toxodontia*, from which they are distinguished by the teeth being rooted, completely enamelled, and never prismatic. The upper teeth are also almost always as broad as they are long, and have a small crochet, which, however, through fusion with the cusps on the inner side of the ectoloph, soon becomes inconspicuous. The lower molars are more massive than those of Toxodonts. The molars usually have in addition a cingulum, which is developed in the upper teeth on the anterior, posterior and often also on the inner and outer margins, but in the lower molars only on the outer margin. A cingulum is never present in the *Toxodontia*.

The skull is known only in *Notostylops*, *Leontinia* and *Homalodontotherium*, and in general resembles that of *Nesodon*. The nasal opening is, however, much more deeply incised than in Toxodonts. The mastoid region of *Homalodontotherium* is much less inflated, and the muzzle of *Notostylops* is much shorter and more pointed than among Toxodonts. The skeleton of *Homalodontotherium* is known only by the calcaneum, astragalus, humerus, ulna and tibia, together with the manus and pes. The humerus has a well-developed deltoid crest and a faint trace of the entepicondylar foramen; it is also very broad at its distal end. Ulna and tibia are quite stout, and the latter at the same time very short. Manus and pes have each five digits, the metacarpals are extremely slender, the metatarsals short and stout.

Family 1. **Notostylopidae** Ameghino.

$\frac{3.1\text{-}0.\ 4.\ 3.}{1.1\text{-}0.4\text{-}3.3.}$. *$I_1$ enlarged in both jaws. I^2, I^3 and the upper canine are reduced, I_2, I_3 and the canine of the lower jaw are lacking. Premolars molariform, the upper ones having, however, only one inner cusp. Upper molars much broader than long, without crest but with crochet. The posterior inner cusp of the lower molars is very weak. All of the teeth are brachyodont. Snout short and pointed. Occiput broad, with inflated mastoids.*

This early specialised family has left no descendants. It becomes extinct at the close of the Eocene.

Notostylops Ameghino (Fig. 325). $\frac{3.1.3.3.}{3.1.3.3.}$. *Catastylops* Ameghino. With

four upper premolars. *Pliostylops* Ameghino. With four lower premolars.

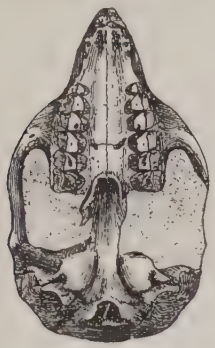


Fig. 325.

Notostylops murinus Ameghino. Upper Eocene (Notostylops beds), Patagonia. Skull, palatal aspect. 1/3. (After Ameghino.)

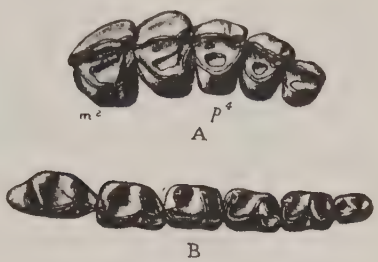


Fig. 326.

Entelostylops triplicatus Ameghino. Upper Eocene (Notostylops beds), Patagonia. *A*, Upper cheek teeth. *B*, Lower cheek teeth. 1/1. (After Ameghino.)

Homalostylops Ameghino. With complete dentition. *Eostylops*, *Entelostylops* (Fig. 326), etc., Ameghino. Eocene; Notostylops beds of Patagonia.

Family 2. **Isotemnidae** Ameghino.

$\frac{3.1.4.3.}{3.1.4.3.}$ *Teeth in compact rows and gradually passing from one form to the next, only the upper canine becomes enlarged at times. Cheek teeth moderately hypsodont; upper premolars and molars with several cusps and crests on the inner side of the ectoloph, and with crochets on the metaloph. Lower premolars and molars with a very well-developed, compressed cusp on the inner end of the anterior crescent.*

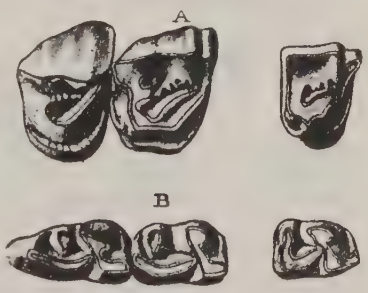


Fig. 327.

Pleurostylodon biconus Ameghino. Upper Eocene (Notostylops beds), Patagonia. *A*, Upper fourth premolar and second and third molars. *B*, Corresponding lower teeth. 1/1.

Isotemnus Ameghino. Canine small, upper premolar triangular, molar oblong. Eocene; Notostylops beds of Patagonia.

Pleurostylodon Ameghino (Figs. 309 A, 327). *Tychostylops*, *Plexotemnus*, *Dialophus* Ameghino, etc. Eocene of Patagonia.

Eochalicotherium Ameghino. Broad lower molars. Eocene of Patagonia.

Trimerostephanus Ameghino. Oligocene; Astraponotus beds. Lower Miocene; Pyrotherium beds.

Pleurocoelodon, *Lophocoelus* Ameghino. Lower Miocene. Pyrotherium beds.

Family 3. **Leontiniidae** Ameghino.

$\frac{3.1\text{-}0.4.3.}{3.1\text{-}0.4.3.}$ *Upper I^2 and lower I_3 enlarged, canines small, sometimes lacking, the premolars and molars intergrading, the upper molars somewhat longer than broad*

and without parastyle. Ridges of the inner side fused. Skull stout, with broad occiput and massive, widely projecting zygomatic arch and nostrils deeply incised between the thickened premaxillaries and the somewhat upwardly directed nasals. The terminal phalanges are developed as broad hoofs, the astragalus and calcaneum are stout and similar to those of Nesodon (according to Gaudry).

Leontinia Ameghino. With canine. *Ancylocoelus* Ameghino. Without canine. *Henricofilholia* Ameghino. Lower Miocene; Pyrotherium beds.

Colpodon Burm. Miocene; Colpodon beds.

Carolodarwinia, Stenogenium Ameghino. Oligocene (Astraponotus beds) and Lower Miocene.

Family 4. **Homalodontotheriidae** Lydekker.

(*Ancylopoda* Zittel, *partim.*)

$\frac{3.1.4.3.}{3.1.4.3.}$ *Canines enlarged in both jaws, all of the remaining teeth intergrading and very closely apposed, brachyodont. Upper molars are broader than long, without spur on the inner side of the ectoloph but with outer and inner cingulum, the lower molar having only an outer cingulum. Skull with a small brain-case, slightly*

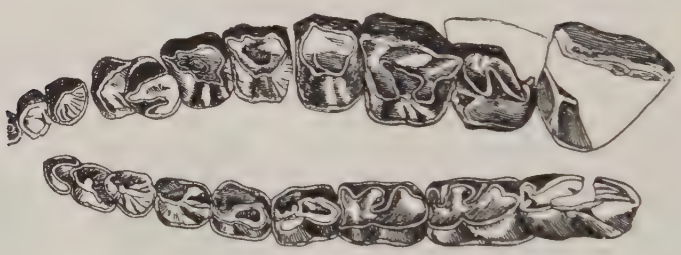


FIG. 328.

Homalodontotherium cunninghami Flower. Upper Miocene (Santa Cruz beds), Rio Gallegas, Patagonia. Upper and lower cheek teeth. $^2/_5$. (After Flower.)

inflated in the mastoid region, short nasals, remotely situated and massive zygoma. Manus with five slender metacarpals and retractile claws, cleft at the ends. Pes with five short metatarsals, long calcaneum and distally rounded astragalus.

Homalodontotherium Flower (Fig. 328). Upper molars rounded and trapezoidal. Humerus massive, with broad distal end and a long deltoid crest. Tibia short and thick-set. Miocene; Santa Cruz, Patagonia.

Thomashuxleya Ameghino. Upper molars are rounded and very broad. Eocene; Notostylops beds of Patagonia.

Proasmodeus Ameghino. Oligocene; Astraponotus beds. *Asmodeus* Ameghino. Upper molars quadrangular. Lower Miocene; Pyrotherium beds.

Diorotherium, Prochalicotherium Ameghino. Lower Miocene; Pyrotherium beds.

Suborder D. ASTRAPOTHERIOIDEA Ameghino.[1]

(*Amblypoda* Ameghino.)

Medium-sized to large herbivores with brachyodont dentition, spatulate incisors and tusk-like canine. Premolars, at times also the incisors, partly atrophied, and smaller than molars. Upper molars, as a rule, longer than broad, with a parastyle, and often also with a crest on the ectoloph, with slightly curved protoloph and a short metaloph. Lower molars with two unequally long crescents and two inner cusps, of which the first is inwardly connected with the posterior extremity of the first crescent, and the second later becomes fused with the anterior end of the second crescent. Astragalus with flat articulation for the tibia.

The *Astrapotherioidea* are closely allied to the *Entelonychia*. They are distinguished from the latter principally by the tusk-like canine and usually by the form of the molars, which are somewhat like those of the rhinoçeros. There is no inflation of the squamosal region, at least not in *Astrapotherium*. The *Trigonostylopidae* are most nearly related to the *Entelonychia*, and differ from them only in the shape of the incisors and canines, in the very brachyodont and simple molars. The astragalus, at first convex, becomes flattened as the weight of the animal increases, and loses almost entirely its mobility.

Family 1. Trigonostylopidae Ameghino.

$\frac{?\,1.4.3.}{?\,1.4.3.}$ *Incisors small, canines well developed. There is a long diastema in front of and behind the conical first premolar. Upper premolars and molars with rounded triangular or quadrangular shape, very simple, with a parastyle, ectoloph, protoloph, and rudiment of a metaloph. Lower premolars and molars composed of a short oblique transverse ridge and one crescent, at the posterior end of which there is a small inner cusp. Astragalus with a rather long neck.*

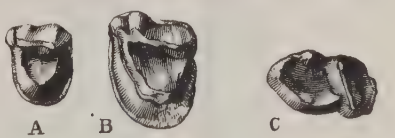


Fig. 329.

Trigonostylops wortmani Ameghino. Upper Eocene (Notostylops beds), Patagonia. *A*, Upper fourth premolar. *B*, Upper molar. *C*, Lower third molar. 1/1.

The *Trigonostylopidae* have the simplest and lowest molars of all South American mammals of the Tertiary. Descendants of this family are unknown. It becomes practically extinct in the Oligocene.

Trigonostylops (Fig. 329), *Pleurystylops* Ameghino. Upper molars triangular. Eocene; Notostylops beds.

Pseudostylops, Edvardocopeia Ameghino. Upper molars quadrangular. Oligocene; Astraponotus beds.

[1] *Ameghino, Florentino*, Sur les ongulés fossiles de l'Argentine. Revista del Jardin zoologico Buenos Aires, 1894.—Notices préliminaires sur des ongulés nouveaux des terrains crétacés. Bol. Acad. Nacion. de Cienc. de Cordoba, vol. xvi., 1901.—*Gaudry, A.*, Mém. Soc. Géol. France, Paléont. vol. xii., 1904. Annales de Paléontologie, 1906.—*Lydekker, R.*, Annales del Museo de La Plata. Paleontología, vol. ii., 1892.

Family 2. **Albertogaudryidae** Ameghino.

$\frac{3.1.4.3.}{3.1.4.3.}$. *Upper molars broader than long, slightly quadrangular, with short protoloph and a detached inner cusp. Lower premolars and molars consisting of two crescents and a detached inner cusp. Incisors not well developed, upper canines triangular. Premolars simpler than molars. Astragalus with a short neck.*

The members of this family, which are ancestral to the next to be considered, attained the size of a tapir, and were among the largest of all South American Eocene mammals.

Albertogaudrya, Ruetimeyeria Ameghino. Upper molars rounded. Eocene; Notostylops beds.

Scabellia Ameghino. Upper molars quadrangular. Eocene; Notostylops beds.

Family 3. **Astrapotheriidae** Ameghino.

$\frac{3.1.3\text{-}2.3.}{3.1.2\text{-}1.3.}$. *Incisors small, especially the upper ones, which are cleft and have two lobes. Canines developed as powerful, triangular tusks, whose tips close against each other. Premolars are simpler and smaller than the molars and are fewer in number. Upper molars are longer than wide and consist of a straight ectoloph, an oblique protoloph and a short straight metaloph, also having a parastyle and crest. M^3 without metaloph. Lower molars consist of two elongated crescents and an inner cusp which is sometimes fused with the anterior end of the second crescent. Manus and pes pentadactyl. Astragalus flat and with very short neck.*

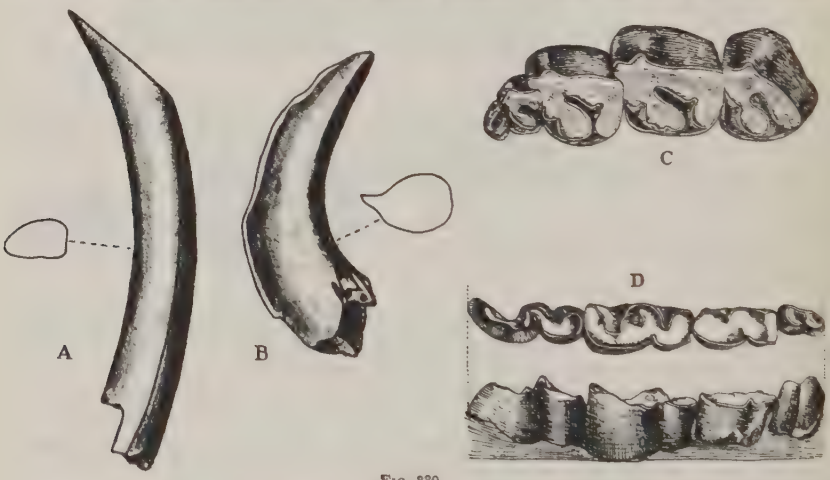


FIG. 830.

Astrapotherium magnum Ameghino. Upper Miocene (Santa Cruz beds), Patagonia. *A*, Upper canine. *B*, Lower canine, 1/4. *C*, Upper third premolar to third molar. *D*, Lower fourth premolar to third molar, 1/3. (After Ameghino.)

These large ungulates, with dentition simulating that of rhinoceroses,

more especially *Metamynodon*, have a rather short skull with a broad forehead, broad palate and narrow cranium, but lacking the usual characteristic among notungulates of an inflated mastoid region. The humerus has a deltoid crest extending far down the shaft, and a low, simple trochlea, but no entepicondylar foramen. The ulna is well developed, the femur is compressed antero-posteriorly and has a lamella-like third trochanter; is not much longer than the rather slender tibia, which is not fused with the fibula. The calcaneum is short and stout. The flattened, broad astragalus articulates closely with the fibula and cuboid, and is very similar to the astragalus of amblypods. Manus and pes are pentadactyl. The metapodials are short and stout. The terminal phalanges were apparently short, broad hoofs. In the milk dentition $\frac{4}{3}$ *D* are still present.

Astrapotherium Burm. (*Mesembriotherium* Moreno; *Listriotherium*, *Xylotherium* Mercerat) (Fig. 330). $\frac{2}{1}$ premolars. Of this genus only, the skull and extremities are known. Miocene of Patagonia.

Astrapothericulus Ameghino. Miocene.

Parastrapotherium Ameghino. $\frac{3}{2}$ premolars. *Liarthrus* Ameghino. Lower Miocene; Pyrotherium beds.

Astraponotus Ameghino. Supposed to have complete dentition. Oligocene.

Proplanodus Ameghino. Eocene; Notostylops beds.

Suborder E. PYROTHERIA.[1]

Skull short and anteriorly elongated. Dentition reduced. $\frac{2.?\,0.3.3.}{1.\ 0.2.3.}$ *Lower incisors long and stout, projecting forward. Cheek teeth each with two parallel transverse ridges. Bones of the extremities stout. Extremities presumably pentadactyl.*

The *Pyrotheria* are restricted to the lower Tertiary of Patagonia, and comprise the largest of all South American ungulates. They appear first in the Notostylops beds, and become extinct after attaining their maximum development in the Pyrotherium beds.

The skull must have been short because the cheek teeth begin near the tusk-like incisors. The orbits in the adult are situated above the fourth premolar. The dentition lacks one upper incisor. P^2 is triangular and consists of two outer and two small inner cusps, P_3 has an anterior cusp and a cross ridge. All of the remaining premolars are similar to the molars and have two parallel cross ridges and a basal cingulum, which on the upper molars is on the outer and anterior surface and on the lower on the inner and posterior surface. The lower jaw exhibits a broad ascending ramus and a weak slender coronoid process.

The scapula has a well-developed coracoid process. The humerus and femur are much longer respectively than the forearm and lower leg. The humerus is antero-posteriorly compressed, without entepicondylar foramen, but with a very prominent epicondylar crest on both sides, and with well-developed exterior deltoid crest. According to Gaudry, this specialisation points to digging habits and great mobility of the digits.

[1] *Ameghino, Florentino*, Mammifères crétacés de l'Argentine. Boletin del Instit. Geografico Argentino, 1897.—Linea filogenética de los Proboscideos. Anales del Museo Nacional, Buenos Aires, 1902.—*Gaudry, A.*, Fossiles de Patagonie. Annales de Paléont., Paris, 1909.

Radius short and fused with ulna. Olecranon high. Ilium joined to the sacrum for a considerable distance. Femur with only first trochanter, but with high head. This bone and the tibia are placed in the same vertical line one over the other. The fibula is fused with the tibia above and below. The astragalus is flattened and has a smooth tibial facet directly adjoining those for the navicular and calcaneum. The navicular is entirely underneath the astragalus, which possibly gives rise to the vertical arrangement of the toes.

The teeth as well as the bones of the extremities are similar to those of the *Proboscidea*, especially *Dinotherium*, and for this reason Ameghino traces the origin of the *Proboscidea* back to *Pyrotherium*. In dental structure there is also a great likeness to *Diprotodon*. There can, however, be no relationship between this form and either the Marsupials or the Proboscideans. The origin of the *Pyrotheria* is at present wholly unknown.

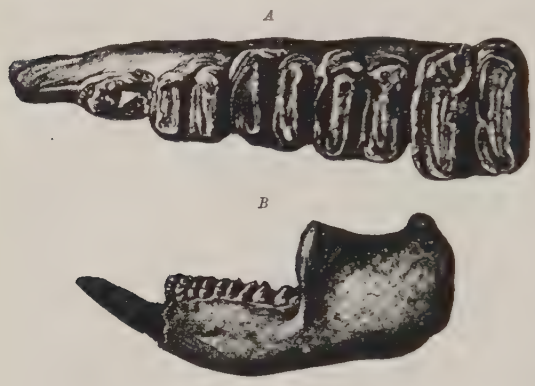


FIG. 331.

Pyrotherium romeroi Ameghino. Lower Miocene, Patagonia. *A*, Upper cheek teeth, grinding surface, 1/4. *B*, Lower jaw, left lateral aspect, 1/12. (After Gaudry.)

Pyrotherium Ameghino. $\frac{2.\,?\,0.3.3.}{1.\ 0.2.3.}$ (Fig. 331). The ridges of the quadrangular molars are at right angles to the tooth row, posteriorly convex on the lower, and anteriorly convex on the upper molars. Lower Miocene of Chubut, Patagonia. *P. romeroi* Ameghino.

Propyrotherium Ameghino. Smaller than the preceding form. Oligocene; Astraponotus beds. *P. saxeum* Ameghino.

Carolozittelia Ameghino. Lower incisor with long root. Upper molars rounded with two posteriorly directed ridges. Lower molars oval, with two ridges almost at direct right angles to the tooth-row. M_3 with third ridge. About the size of a tapir. Upper Eocene; Notostylops beds of Patagonia.

Ricardowenia, *Paulogervaisia* and *Archaeolophus* Ameghino. Very problematic remains.

Order IX. SUBUNGULATA.

Usually large, plantigrade or digitigrade herbivores or animals adapted for aquatic life, having originally a complete brachyodont-bunodont dentition. A pair of incisors are enlarged in early forms, often developing into tusks, the remaining incisors and canines reduced, entirely lacking or gradually passing into one another. The molars are practically quadritubercular, the upper ones equally as long as broad. The premolars are very like the molars. Bones of carpus and tarsus slightly alternating

or serial; centrale often present. Extremities specialised in various ways, and in aquatic forms the posterior pair is totally reduced. Skull elongated and low, with a broad parietal region. Uterus bicornuate, placenta zonal, usually deciduous.

On account of the high degree of specialisation which the skeletal elements have undergone in the different suborders, a more precise diagnosis is impossible. The suborders appear almost contemporaneously in Egypt, being represented by forms with a low skull, a broad occiput, well-developed sagittal crest and a narrow cranium, and usually the enlargement of a pair of incisors, combined with a reduction of the remaining incisors and canines. The molars are bunodont, brachyodont and practically quadritubercular. Their cusps are combined in pairs to form ridges which become crescent-shaped in the lower jaw. The premolars become molariform in early forms, and the incisors, canines and premolars gradually pass into one another when one pair of incisors is not enlarged. Also the development of the base of the skull is very much alike in all of these forms.

The extremities show very varied lines of development even in the oldest Subungulates. The oldest *Hyracoidea*, apart from their bunodont dentition, have all the external characteristics of recent forms; on the other hand, the genus *Moeritherium* approaches the primitive *Proboscidea* and *Sirenia*, not only in dentition, but also in the structure of the humerus, scapula and pelvis, so that the common ancestor of both can not be far removed. The *Embrithopoda* show, in spite of their very different dentition, so great a similarity in foot-structure to the *Proboscidea* that a common ancestor, although rather remote, is certain.

That all four suborders must have arisen from a common bunodont form long before the Upper Eocene, is shown among other characteristics by the lack of the primitive feature of the entepicondylar foramen of the humerus. Relationship to the *Notoungulata* must be absolutely excluded, for the dentition of these South American forms originated directly from a secodont ancestor, whereas the ancestor of the *Subungulata* must have had a bunodont dentition, from which we might easily infer a close relationship to the *Condylarthra*.

Suborder A. EMBRITHOPODA Andrews.

Huge herbivores with lophodont molars. Fore limbs similar to those of the Proboscidea. Hind limbs like those of the Amblypoda. Oligocene of Egypt.

Family 1. **Arsinoitheriidae** Andrews.

Huge ungulates with a pair of large bony horns on the nasals and two smaller ones on the frontals. Short, high snout with nares divided anteriorly. Parietal region inclined forward, with a large supraoccipital swelling. Orbits open posteriorly. Dentition complete. Incisors, canines and premolars passing from one form to the other and set very closely together. Premolars simpler than the molars. Upper and lower molars made up of two V*-shaped ridges, whose anterior branch is shorter than the other. Humerus and femur long and massive. Tibia and fibula short; ulna much thicker than the radius. Astragalus flat with slightly*

raised trochlea and with articular surface for the cuboid. Fore and hind limbs very short and with five digits.

The *Arsinoitheriidae* are restricted to the Oligocene of Egypt. The skull is of about the same size and very similar in form to that of the rhinoceros, except that in these adults the nares are divided by a bony plate. The high horns placed on the nasals recall those of the *Titanotheriidae*. The ascending ramus of the lower jaw is very high and narrow. The teeth are very compact and pass gradually from the chisel-shaped incisors to the fourth premolar. The upper premolars have a straight ectoloph and an oblique transverse ridge, the lower ones consist of two small strongly compressed crescents. They are on the whole very short and differ considerably in this respect from the molars. The molars consist of two V-shaped crescents, whose anterior branch forms a very sharp edge, whereas the posterior one is a broad, high, somewhat oblique backwardly directed ridge. When worn down by grinding, this becomes in appearance an entoloph. The lower molars recall those of *Coryphodon*, the upper those of *Uintatherium*. The two posterior teeth of the milk dentition are very like the molars.

The bones of the extremities are extremely stout. The scapula is broader than high, the humerus has a very large deltoid crest, but no entepicondylar foramen. The ulna is much thicker than the radius and has a huge olecranon. It rests partly on the lunar. The pelvis is distinguished by the extremely large ilium. The femur, which is antero-posteriorly compressed, has one large trochanter. The bones of the fore limb are more like those of *Uintatherium*, those of the hind limb like those of *Elephas*. The arrangement and form of the carpals, tarsals and metapodials are practically the same as in *Elephas*, only the astragalus differs in having an articular surface for the cuboid. There is, at all events, a distant relationship between these forms and the Proboscidea.

The only known genus is *Arsinoitherium* Beadnell (Fig. 332) from the Oligocene of Egypt, having for type species *A. zitteli* Beadnell.

Suborder B. HYRACOIDEA.[1]

Incisors long, vertically placed, rodent-like; the lower first and second incisors chisel-shaped. Premolars more or less molariform. Molars ranging from bunodont to lophodont, with four roots. Lower surface of the zygomatic arch has special articular surfaces for the lower jaw. Ascending ramus of the lower jaw very broad, with slender coronoid process and a foramen behind the third molar. Humerus without entepicondylar foramen. Extremities plantigrade or semidigitigrade. Manus with four digits, pes with three. Carpus serial with freely articulating centrale. Astragalus distally truncated, with excavated trochlea and a deep, pit-like articular surface for the malleolus tibiae.

The *Hyracoidea* were until very recently represented only by the small forms of the genus *Hyrax*, which was at first associated with rodents on

[1] *Adloff, P.*, Zahnsystem von Hyrax. Zeitschr. f. Morph. und Anthrop., 1902.—*Andrews, C. W.*, Catalogue, 1906. Geological Magazine, 1908.—*Brandt, J. F.*, Untersuchungen uber die Klippschliefer (*Hyrax*). Mém. Acad. Impér. Sci. St-Pétersbourg, 1869, 6 sér., vol. xiv.—*Major, C. I. Forsyth, Pliohyrax graecus* from Samos. Geological Magazine, 1899.—*Schlosser, M.*, Säugetiere aus dem Oligocän von Ägypten. Beitr. Palaont. Öst.-Ungarns und des Orients, 1911.

account of the structure of the incisors and the form of the skull. Cuvier pointed out the similarity of the teeth and extremities to those of rhinoceros,

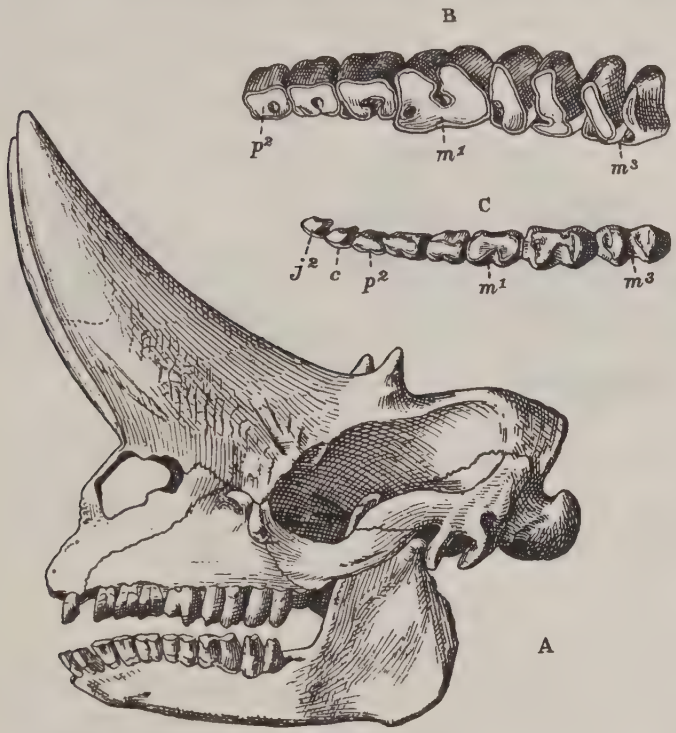


FIG. 332.

Arsinoitherium zitteli Beadnell. Oligocene, Fayum, Egypt. *A*, Skull and lower jaw, 1/9. *B*, Upper cheek teeth. *C*, Lower cheek teeth, 2/9. (After Andrews.)

and Cope instituted the order *Taxeopoda* for the reception of *Hyrax* and other ungulates on account of the serial order of the carpals.

The *Hyracoidea* are subdivided into the families *Hyracidae*, *Saghatheriidae*, and *Myohyracidae*.

Family 1. **Hyracidae** Gray.

$\frac{1.0.4.3.}{2.0.4.3.}$. *Premolars molariform and like the molars are brachyodont and lophodont. Upper molars with* W*-shaped ectoloph and two oblique ridges. Lower molars consisting of two crescents. Roof of the skull flat, snout short.*

The *Hyracidae* inhabit the southern and eastern portions of Africa, Arabia and Syria. Fossil forms are not known. They are distinguished from the *Saghatheriidae* not only by their small size but also by the flattened roof of the skull; by the orbits being placed far forward and usually closed posteriorly; by having two temporal crests in place of one sagittal crest; and by the

shortening of the muzzle, to which is due the loss of the canines, the second and third upper incisors and the third lower incisors. The milk dentition consists of $\frac{2.1.4.}{3.1.4.}$, from which we can infer the former presence of the I_3, I^2, and canines. The extremities are plantigrade, the terminal phalanges distally flattened and with nails.

The cheek teeth of the genus *Procavia* Storr (*Hyrax* Herm., *Heterohyrax* and

FIG. 333.

Procavia (*Dendrohyrax*) *arborea* Smith. Recent, Cape of Good Hope. *A*, Skull and lower jaw, $^2/_3$. *B*, Left upper jaw from below, $^1/_1$.

Dendrohyrax Gray) (Fig. 333) resemble partly those of *Rhinoceros*, and partly those of *Paloplotherium* or *Anchilophus*.

Family 2. **Saghatheriidae** Andrews.

$\frac{3.1.4.3.}{3.1.4.3.}$ *I^1 large triangular in section, lower I_1 and I_2 chisel-shaped, with two notches on the superior surface. Upper canines premolariform, lower canines and I_3, as well as I^2 and I^3 peg-like or premolariform and usually separated from one another by diastema and also from the front incisors and canines. Premolars are as a rule simpler than the molars, but the upper ones usually have four cusps, or have a complete anterior transverse ridge and a short posterior one. Upper molars with* W*-shaped ectoloph, having parastyle and mesostyle and two oblique ridges formed from a small loph and a low inner loph. Lower molars with two more or less distinct outer crescents and two inner cusps. M_3 always with a third crescent. Snout usually long and narrow, cranium convex with sagittal crest. Orbit situated very far back and not completely closed. Lower jaw high, with broad canal underneath the dental row, which opens under M_3. Lateral toes are shorter and thinner than the middle toes. Carpals, high and narrow. Distal articulation of astragalus faintly convex.*

The *Saghatheriidae* appear first in the Oligocene of Egypt and display an unusual variety of forms. In size they range between that of a fox and tapir. In dentition they vary from bunodont, pig-like (*Geniohyus*) and lophodont, with *Paloplotherium*-like molars (*Saghatherium*). The upper molars of *Geniohyus* and *Bunohyrax* are similar to those of the *Anthracotheriidae*, and the upper molars of *Megalohyrax* to those of *Palaeotherium*. In Egypt the *Saghatheriidae* soon become extinct, only the genus *Saghatherium* having a descendant in the Lower Pliocene genus *Pliohyrax*.

Geniohyus Andrews. Premolars simple, lower molars pig-like, the upper ones *Brachyodus*-like. · *G. mirus* Andr.

Bunohyrax Schlosser. Premolars complex, upper ones rounded and triangular. Lower molars with true crescents.

Mixohyrax Schlosser (Fig. 334). Upper premolars quadrangular. Molars lophodont. *M. niloticus* Schl.

Pachyhyrax Schlosser. Spurs on the ridges of the upper molars.

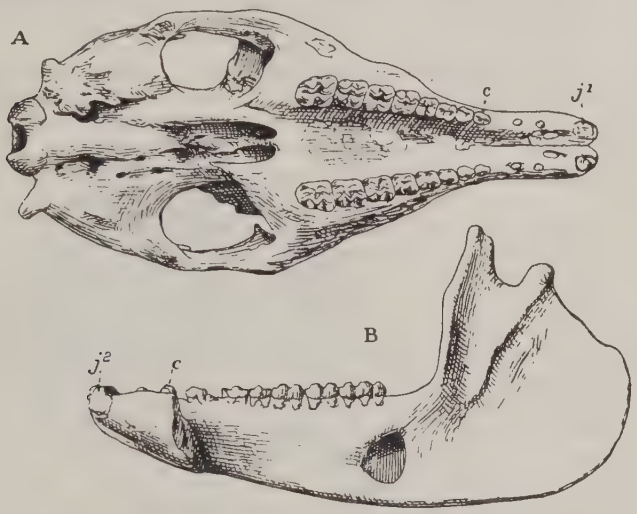


FIG. 334.

Mixohyrax niloticus Schlosser. Oligocene, Fayum, Egypt. *A*, Skull, palatal aspect. *B*, Right ramus of lower jaw from within. 1/4.

Saghatherium Andrews. The size of a sheep. Upper premolars much simpler than the molars; upper molars lophodont, lower ones lophoselenodont. Diastema very short. *S. antiquum* Andr.

Megalohyrax Andrews. The largest of all *Saghatheriidae*. Premolars almost entirely like the molars. *M. eocaenus* Andr.

Pliohyrax Osborn (*Leptodon* Gaudry). Lower jaw without diastema. I_3, both canines as well as I^2 and I^3 are premolariform. Lower Pliocene of Pikermi and Samos. *P. graecus* Gaudry sp.

Family 3. **Myohyracidae** Andrews.

Molars extremely hypsodont, but with distinct roots.

Myohyrax Andrews. Known only by part of the dentition. Pattern of molars resembling that of much-worn molars of the more hypsodont species of *Hyrax*. *M. oswaldi* Andrews, as big as a large rat, from Lower Miocene, Kachuku, British East Africa.

Protypotherioides Stromer. Species larger than *M. oswaldi*. Miocene, S.W. Africa.

Suborder C. PROBOSCIDEA.[1]

Large five-toed, usually tall-limbed, semidigitigrade herbivores with proboscis. Skull large, usually with large air-cells. At first there is a pair of enlarged upper and lower incisors; finally only one pair above. Canines present only in primitive genera. Cheek teeth at first bunolophodont, then lophodont, and in the final stage consisting of narrow, transverse lamellae. Femur almost always without third trochanter. Carpals serially arranged. Astragalus broad with slightly convex trochlea. Calcaneum articulating with fibula.

The origin of the *Proboscidea* has remained obscure until recently, although Blainville suspected that they were related to the *Sirenia*. This conjecture has been confirmed by recent discoveries in the Oligocene of Egypt, which show that the earliest forms have among other characteristics a large number of teeth, the cheek teeth and also the cranial structure being similar to those of the *Sirenia*.

The dentition of the *Proboscidea* consists only of incisors and cheek teeth, except in the case of the *Moeritherium*, but even in this form a pair of incisors has become enlarged. Soon the remaining incisors disappear entirely and the single enlarged pair develops into enormous tusks. In the later species of *Mastodon* even this last remaining pair is lost in the lower jaw. The tusks are composed of dense elastic ivory, which is seen in cross-section to be traversed by fine lines extending from the centre of the tusk to its periphery in two sets crossing each other like the enchased ornament of a watch-case. The proximal portion, in particular, of the tusks is frequently covered with a thin layer of enamel. The teeth are seated in deep alveoli in the premaxillary, and have large, open pulp cavities.

The cheek teeth of recent elephants are distinguished from those of all other ungulates by their large size and numerous compressed transverse ridges, as well as by the thick coating of cement in the valleys between the ridges. These teeth, however, display features in common with the bunolophodont teeth of *Moeritherium*, which are made up of two pairs of cusps joined by a slight ridge and a small talon. In *Palaeomastodon* the number of ridges is increased, but in the lower jaw the number of cheek teeth is reduced by one. In *Mastodon* the reduction of the simultaneously functional teeth is extensive, and there is an increased number of ridges. The number of transverse ridges is even greater in *Stegodon*, which has from 6 to 12, and

[1] *Adams, A. Leith*, British Fossil Elephants. Palaeont. Soc., 1877.—*Andrews, C. W.*, Catalogue, 1906, and Evolution of the Proboscidea. Philos. Trans., ser. *B*, 1903.—*Bach, F.*, Mastodon aus Steiermark. Beitr. z. Palaont. Ost.-Ungarns, vol. xxiii., 1910.—*Cope, E. D.*, The Proboscidea. Amer. Naturalist, 1889.—*Depéret, Ch.*, Archives du Musee de Lyon, 1887, vol. iv.—*Falconer and Cautley*, Fauna antiqua sivalensis, 1846, and Palaeont. Mem. ed. by Murchison, 1863, vol. i.—*Kaup, J. J.*, Ossements fossiles de mammifères, 1832-35, Cah. I. and IV., and Akten der Urwelt, 1841, Heft IV. —Beiträge zur Kenntnis urweltlicher Säugetiere, 1857, Heft III.—*Lartet, Ed.*, Bull. Soc. Géol. de France, 1859.—*Lortet and Chantre*, Arch. Mus. de Lyon, vol. i., 1872 ; vol. ii., 1879.—*Lydekker, R.*, Catal. British Mus., vol. v., 1886.—*Meyer, H. von*, Mastodon. Palaeontogr., 1867, vol. xvii.—*Pohlig, H.*, Nova Acta Acad. Carol. Leopold., 1888-91.—*Schlesinger, G.*, Mastodonten. Denkschr. natur. Hofmuseums, Wien, 1917.—Stratigr. Bedeutung europ. Mastodonten. Mitth. geol. Ges. Wien, 1918.—Mastodonten. Geologia hungarica, ii. fasc. 1, 1922.—*Sismonda, E.*, Osteographia di Mastodonte. Mem. Accad. Torino, vol. xii., 1851.—*Vacek, M.*, Österr. Mastodonten. Abh. K. K. Geol. Reichsanst., 1877, vol. vii.—*Weithofer, K. A.* Proboscidier des Arnotales. Beitr. Palaont. Österr.-Ungarns, vol. viii., 1890.

the transverse valleys between them are filled with cement. In *Elephas* the number of ridges increases with each new tooth, and finally becomes 27. The brachyodont teeth of *Moeritherium* and *Stegodon* become hypsodont in *Elephas*. The ridges become plate-like and are joined to one another by means of cement, which in early stages also covers the upper part of the crown. By use the surface of these "elasmodont" teeth becomes flat, and shows broad transverse bands of cement alternating with thin lamellae of enamel and dentine, forming a surface well adapted to the trituration of vegetable food. In *Dinotherium* each cusp becomes joined with the next so as to form narrow, well-defined ridges, similar to those seen in the tapir. Among Mastodons also there are some "tapiroid" forms.

The number of molars is three in each jaw. In front of these there were

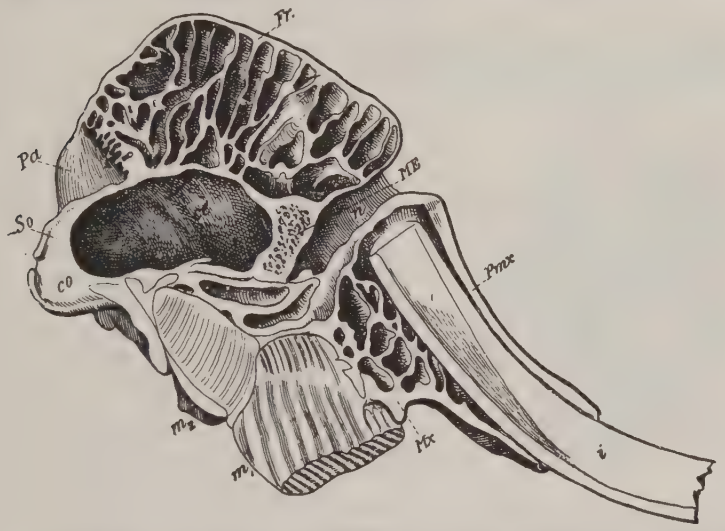


FIG. 335.

Vertical longitudinal section of skull of existing Indian elephant (*Elephas indicus* Linn.). *ce*, Brain cavity; *co*, occipital condyle; *Fr*, frontal; *i*, base of tusk (incisor); m_1, m_2, first and second molars; *ME*, mesethmoid; *Mx*, maxilla; *n*, narial passage; *Pa*, parietal; *Pmx*, premaxilla; *So*, supraoccipital.

originally three premolars, but the number of premolar teeth becomes reduced to two. These teeth are much simpler than the molars and replace the three milk teeth. Premolars are lacking in *Elephas*, *Stegodon* and most species of *Mastodon*. All of the cheek teeth are originally in horizontal rows, and the premolars displace the milk dentition from below. In *Mastodon* there are never more than three teeth functioning at the same time, and in later forms only two, and finally only one. The dental succession takes place during a long interval of time, the newly formed tooth presses upward and forward in an arc and gradually displaces its predecessor. This succession continues during the whole life of the creature, and the cheek teeth are worn down to inconsiderable remnants. The anterior portion of the teeth first becomes worn down by use.

The skull (Fig. 335) exhibits the following modifications in tracing

the series from *Moeritherium* to *Elephas*. The gradual development of the proboscis and tusks brings about a shortening of the maxillary and upward displacement of the nostrils; and this deformation accounts for the high arch of the skull, the formation of air cells and the broadening of the parietal region. The premaxillaries overlap the maxillaries and form large cylindrical sockets for the tusks. The upper jaw becomes deeper and the zygomatic arch weaker. On the other hand, the symphysis of the lower jaw becomes longer, but later on contracts after the lower tusks have been lost. The ascending ramus of the lower jaw becomes higher, but at the same time more slender, and the condyle gradually becomes more elevated.

The extremities of the *Proboscidea* (Fig. 336) are long and pillar-like, and the long bones without marrow cavities. There is no clavicle. The ulna is distally much thicker than the radius. The carpals are more or less serially arranged. A centrale is present in the young elephant. The lateral metacarpals (I and V) are shorter and weaker than the inside ones. The whole foot is encased in a single covering, from which the hoof-like nails of the toes protrude only slightly. The third trochanter of the femur is usually lacking. Tibia and fibula are separated, the latter distally thickened. It articulates with the astragalus and calcaneum. The astragalus has a slightly arched trochlea and articulates distally only with the navicular.

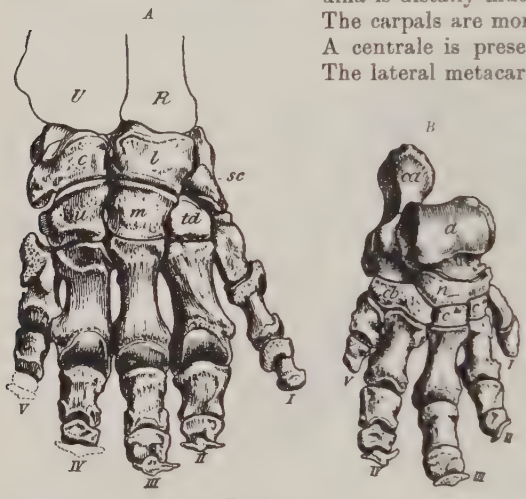


FIG. 336.

Right fore (*A*) and hind (*B*) foot of existing Indian elephant (*Elephas indicus* Linn.) *a*, Astragalus; *c*, cuneiform; *c II.*, *c III.*, second and third cuneiform; *ca*, calcaneum; *ob*, cuboid; *l*, lunar; *m*, magnum; *n*, navicular; *R*, radius; *sc*, scaphoid; *td*, trapezoid; *U*, ulna; *u*, uneiform.

The *Proboscidea* are restricted to the tropical portions of Africa and Asia in recent times. They begin in the Eocene of Egypt, spread over the Northern Hemisphere in the Miocene and reach South America only in the Pleistocene. As index fossils their cheek teeth can be used only with great circumspection, on account of the numerous transitional forms, all closely allied to one another, and on account of the considerable variation in size of the teeth of one and the same genus.

Family 1. **Moeritheriidae** Andrews.

$\frac{3.1.3.3.}{2.0.3.3.}$ *Second incisor above and below enlarged and the upper one developed into an arched tusk. First incisor above and below, and* I^3 *as well as the canine, small. Premolars simpler than the molars, and like these brachyodont. Upper premolars tritubercular, lower premolars composed of two anterior and one*

posterior cusp. Molars with two pairs of cusps each and a talonid. The anterior portion of the lower premolars and molars is higher than the posterior. Skull low, almost flat, with long, slender cranium and massive, projecting zygomatic arch.

The *Moeritheriidae* appear first in the Upper Eocene of Egypt and become extinct in the Oligocene. They indicate in skull structure and in the number and form of the teeth a transitional stage between the *Sirenia* and *Proboscidea*, and show most distinctly that both groups are descended from a common ancestor.

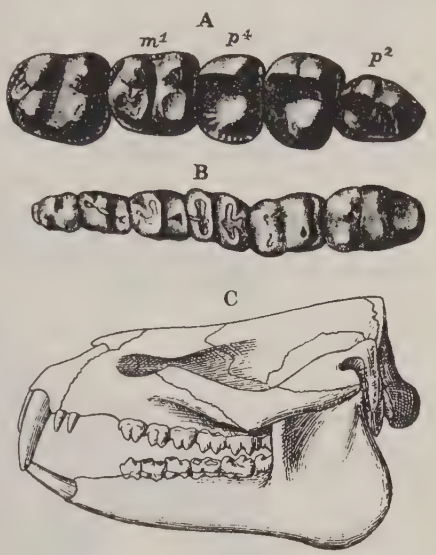


Fig. 337.

Moeritherium lyonsi Andrews. Upper Eocene, Fayum, Egypt. *A*, Upper cheek teeth, 1/2. *B*, Lower cheek teeth, 1/3. *C*, Skull and lower jaw restored, 1/9. (After Andrews.)

Moeritherium Andrews (Fig. 337). Lower incisors chisel-shaped, anteriorly directed, upper incisors and canine almost vertically placed. Second incisor in both jaws enlarged, the upper being developed as a massive, curved tusk. The remaining incisors and canines are relatively small. The incisors and canines are covered with enamel on all sides. Upper premolars with two outer and one inner cusp. Upper premolars triangular. Molars in both jaws with two outer and inner cusps each, the cusps being joined to form transverse ridges. The lower molars with strong, and upper molars with small talonid. Lower premolars with unpaired anterior cusps, anterior mostly higher than the posterior. Nasal openings far forward, indicating a short proboscis, cranial roof almost perfectly horizontal, orbits far forward. Nasal bones short. Frontals and parietals long, cranium slender and low, with saggittal crest. Occiput vertical. Zygomatic arch massive anteriorly and posteriorly, much projecting and ending posteriorly near the occiput. The limb bones are slender. The femur has a third trochanter and the astragalus a relatively long neck. The sacrum becomes reduced gradually posteriorly, which would indicate the presence of a long tail. The ilium is distinguished by its great length and slenderness. It strongly resembles that of Creodonts. The species of this genus attained approximately the size of a tapir. Upper Eocene. *M. lyonsi* Andr. Oligocene. *M. andrewsi* Schlosser.

Family 2. **Barytheriidae** Andrews.

$\frac{1.0.3.3.}{?\ ?\ 3.3.}$ *Lower incisors large, anteriorly directed and separated from the second premolar by a long diastema.* P^2 *triangular,* P^3 *and* P_4 *with a thick*

transverse ridge, the lower premolars similar to the molars, and having two almost straight transverse ridges. M_3 with a third ridge. Lower molars with four roots. The ridges of the upper molars are slightly concave posteriorly. Lower jaw massive, with a broad ascending branch.

Barytherium Andrews. The systematic position of this imperfectly known genus is rather uncertain. In its dentition and form of the lower jaw, which is massive with a broad ascending branch and also in the massive form of body, one is reminded of *Dinotherium*. The distally expanded humerus has an unusually well-developed deltoid crest, and the stout radius articulates to an equal extent with the lunar and scaphoid. Upper Eocene of Egypt. *B. grave* Andrews.

Family 3. **Dinotheriidae.**

$\frac{0.0.2.3.}{1.0.2.3.}$ *Symphysis of the lower jaw downwardly curved, with a pair of backwardly directed tusks. First molars in both jaws with three, the remaining*

Fig. 338.

Dinotherium giganteum Kaup. Lower Pliocene, Eppelsheim, Hesse-Darmstadt. Skull and lower jaw, 1/15. (After Kaup.)

molars with two simple slender ridges, separated by broad valleys. Without cement. All teeth in a single plane. Dental succession normal.

Dinotherium Kaup (Figs. 338, 339). Skull moderately high, occiput sloping backwards, with long premaxillaries and broad frontal. Symphysis of

the lower jaw with a broad furrow in front, sharply bent downwards. The massive incisors directed backward and downward, and sunk in deep alveoli. First molars in both jaws with three, the remaining molars with two transverse ridges, which in the upper teeth are anteriorly convex and in the lower are anteriorly concave. Upper molars are almost quadrangular, three-rooted; lower ones longer than broad. M_3 with strong talonid. Skeleton similar to

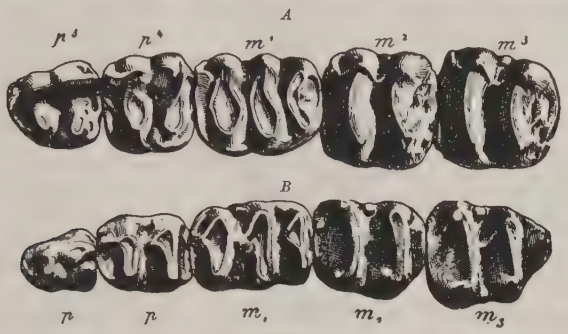


FIG. 339.

Dinotherium bavaricum Meyer. Upper Miocene, Breitenbronn, near Augsburg. *A*, Upper cheek teeth. *B*, Lower cheek teeth. 1/4.

that of *Mastodon*, but with somewhat longer limbs. The larger species of this genus exceed most elephants in size.

In the Lower Miocene of British East Africa, *D. hobleyi* Andrews. In the Upper Miocene of Europe the genus is represented by *D. bavaricum* Meyer (= *D. levius* Jourdan). In the Lower Pliocene of Europe and in Samos (?) is found the type species, *D. giganteum* Kaup.[1] In India other species are known, *D. indicum* Falconer, *D. sindiense* Lydekker.

Family 4. **Elephantidae** Gray.[2]

Superior incisors developed as large straight or curved tusks; inferior incisors smaller, straight, or absent. Cheek teeth very large, composed of more than two crests, the transverse valleys often filled with cement. Premolars generally absent. Dental succession effected by the crushing out of the anterior teeth. In specialised forms jaws moving in a horizontal plane. Oligocene to Recent.

Palaeomastodon (*Phiomia*) Andrews (Figs. 340, 341). $\frac{1.0.3.3.}{1.0.2.3.}$ Molars in a continuous straight line and functioning simultaneously. Upper incisors rather short, laterally compressed and blade-like. Lower incisors elongate spatulate. All the incisors are provided on the outer surface with enamel,

[1] *Andrews, C. W.*, Skull of Dinotherium giganteum. Proc. Zool. Soc., 1921, p. 525.

[2] *Depéret, C., and Mayet, L.*, Les Éléphants pliocènes. Ann. Univ. Lyon, n.s. I., fasc. 42, 1923.—*Dietrich, W. O.*, Elephas primigenius fraasi. Jahresb. Verein f. vaterl. Naturk. Württ., 1912.—Elephas antiquus recki. Wiss. Ergebn. Oldoway Exped., Berlin, 1916.—*Felix, J.*, Das Mammuth von Borna. Veröffentl. städt. Mus. Völkerk., Leipzig, 1912.—*Niezabitowski, E. L.*, Überreste des in Starunia gefundenen Mammuthcadavers. Bull. Acad. Sci. Cracovie, 1911.—Wykopaliska Starunskie, Cracow Museum, 1914.—*Soergel, W.*, Elephas trogontherii u. E. antiquus. Palaeontogr., vol. lx., 1913.—Stegodonten aus Java. *Ibid.*, suppl. 4, 1913.—Elephas columbi. Geol. u. paläont. Abhandl., vol. xviii., 1921.

and have a persistent pulp-cavity. P^2 and P_3 have only one cusp with a small protuberance. P^3 with large outer and small inner cusps. P^4 of the upper and lower jaws has four paired cusps. Molars as in *Tetrabelodon* and *Mastodon*, each have three well-defined transverse ridges consisting of two cusps each. M_3 usually with a talonid. Symphysis of the lower jaw very much elongated. Narial openings high and rather remote. Skull rather high and short, parietals slightly convex, and having a sagittal crest. Oligocene of Egypt. *P. beadnelli* Andrews must have had a fairly long proboscis.

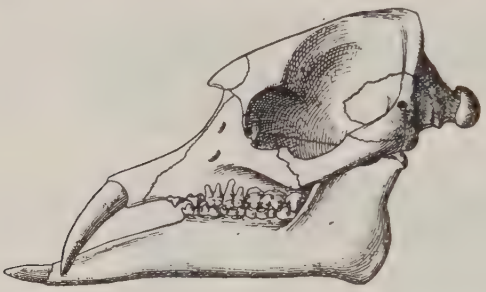


FIG. 340.

Palaeomastodon beadnelli Andrews. Oligocene, Fayum, Egypt. Skull and lower jaw restored. 1/10. (After Andrews.)

Hemimastodon Pilgrim. Teeth intermediate between those of *Palaeomastodon* and *Mastodon*. Lower Miocene, India.

Tetrabelodon Cope (Figs. 342-345). Skull more resembling that of *Elephas* but the frontals are less steeply inclined upward. Upper jaw lower, symphysis of mandible much elongated. Skeleton less elevated and more robust. Dental formula: $\frac{1.0.3.-0.3.}{1.0.2.-0.3.}$. Superior incisors straight or slightly curved downward, with a broad external band of enamel. Inferior incisors smaller and shorter than the upper,

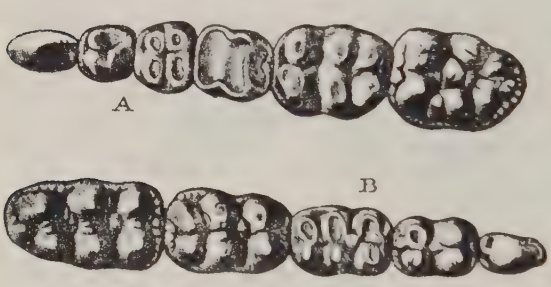


FIG. 341.

Palaeomastodon sp. Oligocene, Fayum, Egypt. *A*, Upper cheek teeth. *B*, Lower cheek teeth. 1/3.

forming a spatulate end to the jaw. Superior cheek teeth large, oblong, quadrate, with three, four, more rarely five high transverse crests, either simple (*Zygolophodon*) or broken up into mammiform bosses (*Bunolophodon*) separated from each other by deep valleys. A median groove divides each transverse crest into two halves and also runs longitudinally throug the entire length of the crown. The whole crown of the tooth is coated with a thick layer of enamel; the cement is also exceptionally developed, yet never entirely fills the transverse valleys. The crowns of the superior cheek teeth are inclined from without inward, and the wear by means of which the dentine is laid bare is stronger on the internal than on the external half of the tooth. The inferior cheek teeth differ from those above merely in their somewhat narrower breadth, the undivided transverse roots beneath the crests, the oblique inclination from without inward, and the stronger wear on the outer half of the crown.

The milk dentition (Fig. 343) has the formula : $\frac{1.0.3.}{1.0.3.}$. The two posterior

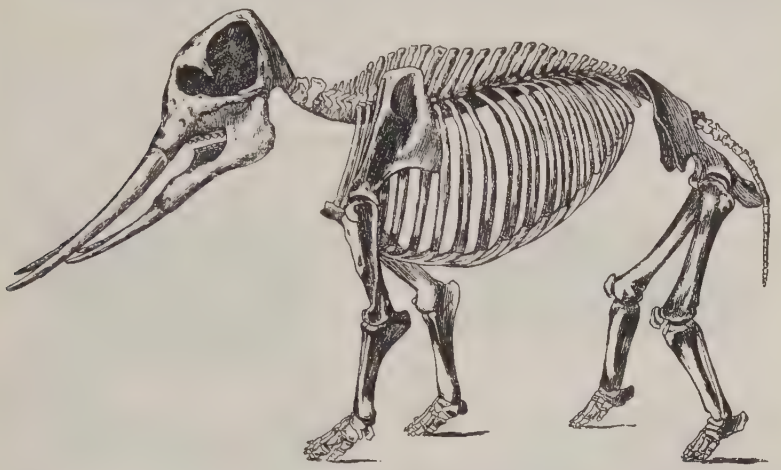


Fig. 342.

Tetrabelodon angustidens Cuvier sp. Middle Miocene, Simorre (Gers), France. Restored skeleton, greatly reduced. (After Gaudry.)

milk molars are sometimes replaced from below by premolars (Fig. 343); in the later species, however, the milk molars succeed each other from behind forward, as in *Elephas*. The last milk molar and the two anterior molars above and below possess an equal

Fig. 343.

Tetrabelodon angustidens Cuvier sp. Middle Miocene, Simorre (Gers), France. Portion of right half of lower jaw, inner aspect, showing third and fourth premolars (p_3, p_4), ready to replace last milk molars (d^2, d^3). 1/4. (After Lartet.)

Fig. 344.

A, *Tetrabelodon angustidens* Cuvier sp. Miocene, Île-en-Dodon. Last lower molar. 1/4. *B*, *Tetrabelodon turicensis* Schinz sp. M. Miocene, Simorre. Last lower molar. 1/5. (After Gaudry.)

number of transverse crests; the last molar is distinguished by an additional crest and frequently by a talon also. In the species of *Tetrabelodon*, therefore,

there are three homogeneous teeth (*dentes intermedii*) in each jaw, which as a rule exhibit three or four transverse crests. Hence they are divided into two sections: *Trilophodon* and *Tetralophodon*.

In the trilophodonts, the number of transverse crests is: $D: \frac{1\text{-}2.2.3.}{1\text{-}2.2.3.}$ ($P: \frac{2.2.}{2.2.}$), $M: \frac{3.3.4.}{3.3.4.}$; in the tetralophodonts: $D: \frac{2.3.4.}{2.3.4.}$ ($P: \frac{2.2.}{2.2.}$), $M: \frac{4.4.5.}{4.4.5.}$. The number of crests may be increased by one in exceptional cases.

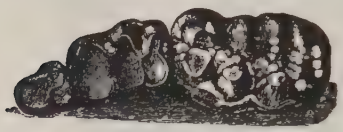


FIG. 345.

Tetrabelodon longirostris Kaup sp. Lower Pliocene, Eppelsheim. The three upper milk molars. 1/3. (After Kaup.)

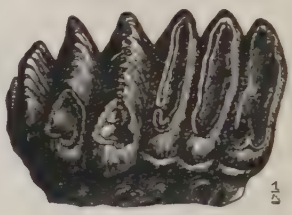


FIG. 346.

Stegodon clifti Falconer and Cautley. Pliocene (or Pleistocene), Burma. First upper molar. 1/4. *c*, Cement; *D*, dentine. (After Clift.)

In the Middle and Upper Miocene of Europe, also in northern Africa, *Tetrabelodon* (*Trilophodon*) *angustidens* Cuvier and *T.* (*Trilophodon*) *turicensis* Schinz are especially abundant. In the Lower Pliocene of Europe (Eppelsheim) *T.* (*Tetralophodon*) *longirostris* Kaup. In the Miocene and Pliocene of North America, several species of *Tetrabelodon* occur, but they need a thorough revision. They include *T. productus* Cope and *T. dinotherioides* Andrews in the Miocene, and *T. mirificus* Leidy and *T. tropicus* Cope in the Pliocene of Texas.

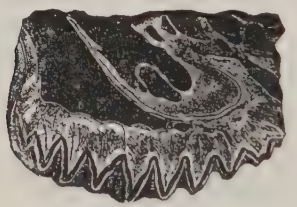


FIG. 347.

Stegodon insignis Falconer and Cautley. Pliocene, Siwalik Hills, India. Vertical longitudinal section of upper molar. 1/6. (After Falconer and Cautley.)

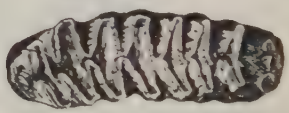


FIG. 348.

Elephas (*Loxodon*) *africanus* Linn. Grinding surface of lower molar. 1/5.

Mastodon Cuvier. Differing from *Tetrabelodon* in having the symphysis of the mandible shortened as in *Elephas*, with not more than functionless remnants of the lower incisors. *M. pentelici* Gaudry and other species occur in the Lower Pliocene of Pikermi, Samos, and Maragha. *M. borsoni* Hays and *M. arvernensis* Croizet and Jobert are characteristic of the Middle and Upper Pliocene of Europe. *M. falconeri*, Lydekker, *sivalensis* Falc. and Cautl., *perimensis* Falc. and Cautl., *punjabiensis* Lydekker, *latidens* Clift and other species are found in the Pliocene (Siwalik formation) of India, also some in China and Japan. *M. americanus* Cuvier has a wide distribution in the Pleistocene of North America. *M. serridens* Cope, and *M. shepardi* and

rugosidens Leidy, are less known. *M. humboldti* Cuvier occurs in Central and South America, being very abundant in the later Pampas formation, while *M. andium* Cuvier is found in western South America.[1] Entire skeletons of *M. americanus* are not especially rare in North America.[2] The synonymous term of *Mammut* Blumenbach is employed by some writers in preference to that of *Mastodon*.

Stegodon Falconer (Figs. 346, 347). A form transitional between *Mastodon* and *Elephas* connected by *M. latidens* with *Mastodon*. Lower incisors absent, upper incisors powerfully developed, without a band of enamel. Molars composed of from six to twelve low, roof-shaped, slightly convex, and usually multipapillose transverse crests, the intermediate valleys being partially filled with cement. In a given jaw, the first and second molars as a rule have an equal number of crests; the teeth of the mandible usually exhibit more

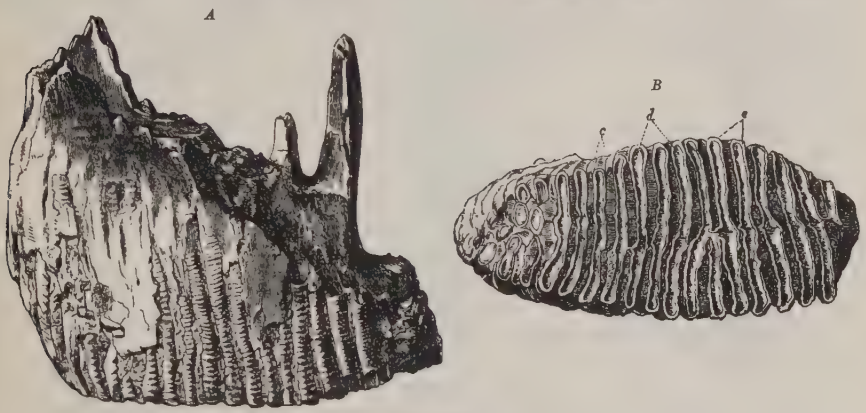


FIG. 349.

Elephas primigenius Blum. Pleistocene, Essex. Upper molar, lateral aspect (*A*), and grinding surface (*B*). 1/5. *c*, Cement; *d*, dentine; *e*, enamel. (After Owen.)

ridges than the corresponding upper molars. Middle and Upper Pliocene of southern and eastern Asia. *Stegodon insignis* Falc. and Caut., *S. bombifrons* Falc. and Caut., and *S. ganesa* Falc. and Caut. Pleistocene of the Narbada Valley and *S. airawana* Martin from Java.

Elephas Linn. (Figs. 348-350). Dental formula: $\frac{1.0.0.3.}{0.0.0.3.}$ (more rarely $\frac{1.0.2.3.}{0.0.2.3.}$). Upper incisors without band of enamel. Molars consisting of from five to twenty-seven deep, compressed transverse plates, with indented superior margin, the intermediate valleys being completely filled with cement, which also covers the entire crown of the tooth. A plane surface is produced through wear. Three milk cheek teeth precede the molars and have somewhat less numerous transverse ridges. In the Indian elephant, the first milk molar is shed in the second year, the second in the fifth year, and the

[1] *Nordenskjöld, E.*, Mastodon andium. K. Svensk. Vet.-Akad. Handl., vol. 37, No. 4, 1903.
[2] *Clarke, J. M.*, Mastodons of New York. New York State Mus. Bull., No. 69, 1902.—*Osborn, H. F.*, Mastodons of the Hudson Highlands. Natural History (New York), vol. xxiii., 1923.

third in the ninth year of life. The first true molar becomes functional in the fifteenth year. Usually only one, or at the most two, cheek teeth are functional in each ramus of the jaw at one and the same time.

The number of transverse plates increases in each new successional tooth, so that the so-called "isomeric intermediate teeth," with an equal number

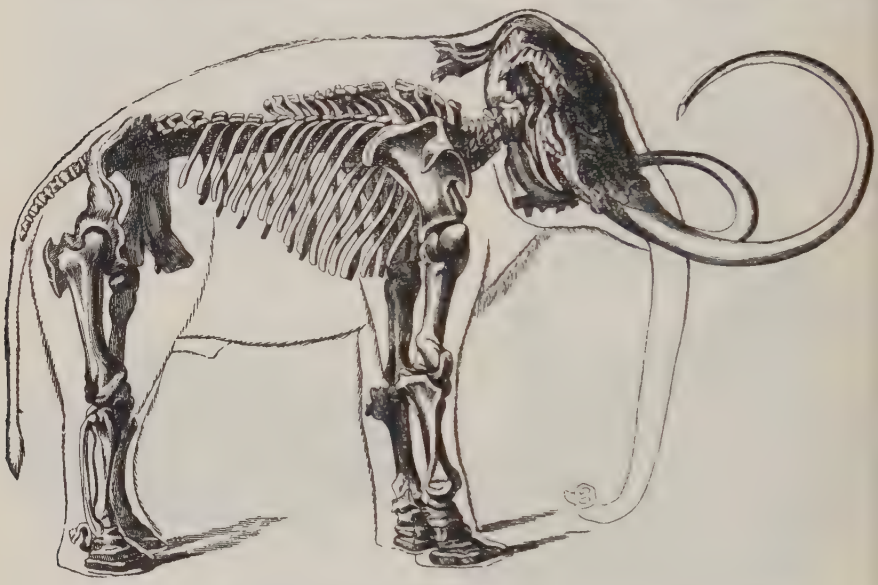


Fig. 350.

Elephas primigenius Blum. Nearly complete skeleton, with remains of soft parts, found in frozen earth in Siberia, greatly reduced. The right and left tusks are transposed in the restoration. Petrograd Museum.

of ridges, which are characteristic of *Mastodon*, are not present in *Elephas*. In the species of *Elephas* accurately known, the ridge formulae are as follows:—

	D_2	D_3	D_4	M_1	M_2	M_3
Elephas africanus	3 / 3	6 / 6	7 / 7	7 / 7	8 / 8-9	10 / 11
,, *planifrons*	3 / 3	6 / 6	7 / 7	7 / 7	8 / 8-9	10 / 10-11
,, *meridionalis*	3 / 3	5-6 / 5-6	7-8 / 7-8	8-9 / 8-9	8-11 / 9-11	10-14 / 11-14
,, *antiquus*	3 / 3	5-7 / 6-8	8-11 / 9-11	9-12 / 10-12	12-13 / 12-13	15-20 / 16-21
,, *hysudricus*	3 / 3	5-7 / 7-9	9-11 / 9-11	9-12 / 9-12	10-12 / 12-13	13-17 / 14-18
,, *indicus*	4 / 4	8 / 8	12 / 12	12-14 / 12-14	16-18 / 16-18	24 / 24-27
,, *primigenius*	4 / 4	6-9 / 6-9	9-12 / 9-12	9-15 / 9-15	14-16 / 14-16	18-27 / 18-27

Falconer divides the genus *Elephas* into two subgenera: *Loxodon* (Fig. 348), with proportionately low and less numerous ridges, which through attrition frequently exhibit a lozenge-shaped pattern; and *Euelephas* (Fig. 349), with

high and numerous, strongly compressed ridges, the anterior and posterior surfaces of which are parallel.

Fossil elephants first appear in the Pliocene of India (*E. planifrons* and *hysudricus* Falconer and Cautley); thence they seem to have spread toward the west, and also occur in the Pliocene of Europe (*E. meridionalis* Nesti). They attained their most extensive geographical range, however, in the later Pliocene and Pleistocene, during which periods they inhabited Europe, northern Africa, Asia, North America and South America. The identification of species is difficult when, as is usually the case, only teeth and incomplete skeletal remains occur.

According to Gaudry, *E. meridionalis* reached a height of about four metres. *E. antiquus* Falconer, which seems to have been equally large, characterises the earlier Pleistocene of Europe, but together with *E. meridionalis* also occurs in the uppermost Pliocene. *E. mnaidriensis* Leith Adams, and *E. melitensis* Falconer from Sicily and Malta, are, according to Pohlig, dwarf races of *E. antiquus*. By far the most abundant species of fossil elephant is the mammoth, *E. primigenius* Blumenbach (Figs. 349, 350). Its powerful tusks are from ten to fifteen feet long, strongly curved outward and upward, and sometimes weigh 250 pounds. The cheek teeth are deep, broader than in *E. antiquus*, the ridges lamelliform, narrow, closely appressed, numerous, and the enamel on the anterior and posterior surfaces less copiously folded. With the exception of Scandinavia and Finland, remains of the mammoth are distributed in the Pleistocene throughout Europe, in northern Africa, northern Asia as far as Lake Baikal and the Caspian Sea; also in China and Japan, and in North America. Entire carcases with long black hair and undercoat of wool have been found in the frozen soil of Siberia. One carcase, preserved in petroleum, was found at Starunia, Galicia. *E. primigenius* is replaced by *E. columbi* Falconer in the middle part of North America, and by *E. imperator* Leidy in the south-western part of the same continent.

Suborder D. SIRENIA. Sea Cows.[1]

Thick-skinned, naked, short-necked, monophyodont herbivorous mammals. Narial openings directed forward. Manus paddle-shaped. Pes absent. Caudal fin horizontal. Two pectoral mammae.

The Sirenians are represented by large aquatic animals, which live on the sea-coast or in the under-current of the larger streams. Their cylindrical body with its horizontal caudal fin, the modification of the anterior extremities into flexible paddle-shaped organs, and the atrophy of the pes recall the

[1] *Abel, O.*, Die Sirenen der mediterranen Tertiärbildungen Österreichs. Abh. K. K. Geol. Reichsanst., 1904, vol. xix. Desmostylus, ein mariner Multituberculate. Acta Zoologica (Stockholm), vol. iii., 1922.—*Andrews, C. W.*, Catalogue of the Tertiary Vertebrata of the Fayum, 1906.—*Capellini, Giov.*, Mem. Accad. Sci. di Bologna, 1872, 3 ser., vol. i. *Ibid.*, 1886, 4 ser., vol. vii.—*Cope, E. D.*, Amer. Naturalist, 1890.—*Depéret, Ch.*, Sitzber. Akad. Wien, 1895.—*Depéret, C., and Roman, F.*, Le Felsinotherium Serresi. Arch. Mus. Hist. Nat. Lyon, 1920.—*Dollo, L.*, Sur les Siréniens de Boom. Bull. Soc. Belge de Géol., 1889.—*Hay, O. P.*, Desmostylus. Proc. U.S. Nat. Mus., Washington, 1915.—*Kaup, J.*, Beitr. zur Kenntnis der urweltl. Säugetiere (Halitherium), 1855, Hefte 2 and 5.—*Lepsius, R.*, Halitherium Schinzi. Die fossile Sirene des Mainzer Beckens. Darmstadt, 1882.—*Matthew, W. D.*, New Sirenian from Porto Rico. Ann. New York Acad. Sci., vol. xxvii., 1916.—*Stromer, E.*, Hüftbeine der Sirenia und Archaeoceti. Sitzber. bayer. Akad. Wiss., München, 1921.—*Yoshiwara, S., and Iwasaki, J.*, Journ. of Imperial University, Tokyo, 1902, vol. xvi.

Cetacea. The structure of the skeleton and their entire organisation, however, leave very little resemblance to the whales to be recognised, and indicate affinity with the ungulates. Skull, teeth and pelvis like those of *Moeritherium*. The affinity with the *Proboscidea* suspected by Blainville is now established with certainty.

In contrast to the light spongy bones of the Cetaceans, the skeleton of the Sirenians is unusually massive in structure, the very dense ribs and vertebrae being especially characterised by a compact, almost ivory-like quality and by considerable weight. The bones of the skull are also in part very dense and the long bones of the extremities are without medullary cavities.

The very short, disk-shaped centra of the cervical vertebrae usually remain distinct. The centra of the dorsal vertebrae exhibit a subtriangular cross-section, are laterally compressed, keeled below, and the spinous processes and zygapophyses are well developed. The number of lumbar vertebrae is from two to three, that of the sacral vertebrae from one to two.

The skull (Figs. 351-353) is characterised by strong zygomatic arches, large squamosal bones, and periotic and tympanic of peculiar form. The parietal and frontal bones form the cranial roof; the nasal bones are reduced, and the narial aperture has moved far backward. The rami of the mandible are deep, robust, and have a high ascending process. The dentition is like that of the ungulates, the lophodont or bunodont cheek teeth fluctuating in number between four and ten. The superior originally sextubercular molars and the inferior quadritubercular molars somewhat resemble those of the tapir and the pig. Absolute distinction between the molars and premolars is never possible, for as a rule no shedding of the teeth occurs. Canines are absent in most of the genera, but sometimes stout incisors are present, especially in the upper jaw.

The bones of the anterior extremities are flexibly united and movable. A clavicle is wanting. The scapula is sickle-shaped. The radius and ulna are equally long and stout. The carpus originally included three ossicles in the proximal series and four in the distal row, but generally several are co-ossified. The five digits have slender metacarpals and the normal number of phalanges. In the *Halitherium-Halicore* series, the pelvis is represented by a long thick ilium and a short broad ischium, but in the manatees the ilium is reduced. In *Eotherium* and young *Eosiren* there still remains a wide obturator foramen between the pubis and ischium. The rudimentary femur, which is concealed in the skin, is merely united with the pelvis by a ligament in later forms.

The two existing genera, *Manatus* and *Halicore*, inhabit the coasts of Africa, India, and Central and South America. Fossil representatives are found from the Eocene onward.

Prorastomus Owen. Dentition apparently complete. Incisor teeth circular in cross-section; superior canine large. Superior molars with two simple transverse ridges directed at right angles to the longitudinal axis of the tooth. Eocene; Jamaica. *P. sirenoides* Owen.

Manatus Rondel. Incisor and canine teeth rudimentary, never functional. From eight to ten cheek teeth above and below on each side, the superior ones three rooted with two transverse ridges and basal cingulum, the inferior ones narrower, with two ridges and talon. In the embryo, traces of three incisors,

one canine, and three premolars are found. Recent, inhabiting the eastern coast of America. Fossil in the Pliocene of South Carolina and Argentina.

Manatherium Hartlaub. Oligocene; Belgium.

Eotherium Owen. Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. Second premolar soon disappearing. Middle Eocene; Egypt.

Eosiren Andrews (Fig. 351). Dental formula: $\frac{3.1.4.3.}{3.1.4.3.}$. Last premolar molariform. Muzzle overlapping. Upper Eocene; Egypt.

Protosiren Abel. Upper Eocene; Egypt.

Halitherium Kaup (*Halianassa* Meyer) (Fig. 352). Skeleton about three

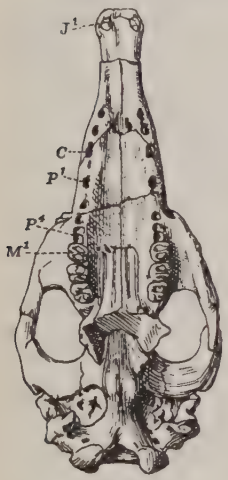


Fig. 351.

Eosiren fraasi Abel sp. Upper Eocene, Fayum, Egypt. Palatal aspect of skull. 1/6. (After Andrews.)

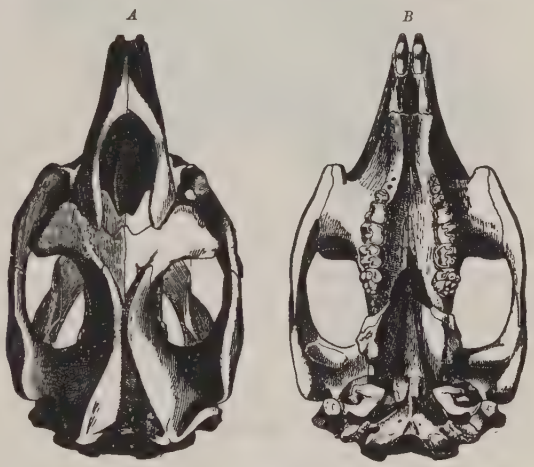


Fig. 352.

Halitherium schinzi Kaup. Oligocene, Flonheim, Hesse Darmstadt. *A*, Skull from above. *B*, Palatal aspect. 1/6. (After Lepsius.)

metres long. Premaxillary curved downwards, with one pair of long cylindrical incisors. Parietal bones long, narrow; frontals short. Nasal bones shield-shaped, short, situated posterior to the large narial aperture. With the exception of the pair of superior incisor teeth, incisors and canines early deciduous. Cheek teeth: $\frac{3.4.}{4.4.}$, bunodont, with warty transverse ridges; the three anterior teeth small, monocuspid, and single rooted, early deciduous. Abundant in the Eocene; Ronca, Italy. *H. veronense* de Zigno. Oligocene; Mayence Basin, Switzerland and France. *H. schinzi* Kaup. Miocene. *H. christoli* Fitzinger.

Metaxytherium Christol. Like *Halitherium*, but only from four to five cheek teeth. Miocene. *M. cuvieri* Christol, *M. krahuletzi* Depéret. Pliocene. *M. serresi* Gervais.

Felsinotherium Capellini (Fig. 353). Dental formula: $\frac{1.0.5.}{0.0.5.}$. Second pre-

molar molariform. Premaxillaries and symphysis of the mandible robust, curved downward. Cheek teeth bunodont. Pliocene; Italy. *F. forestii* Capellini.

Miosiren Dollo. 1.0.3.4.; Miocene, Belgium. *Rhytiodus* Lartet. 1.0.1.4.; *Prohalicore* Flot. Miocene, France.

Desmostylus Marsh. Dental formula: $\frac{0.1.2.2.}{1.1.2.2.}$. Nasal opening far in advance of orbits. Two lower incisors rather long, directed forward. Upper canines developed as tusks. Molars large, consisting of five to eight vertical cylinders fused together in rows. Miocene; Japan and Pacific coast of North America. *D. hesperus* Marsh.

Fig. 353.

Felsinotherium forestii Capellini. Pliocene, near Bologna. Skull and lower jaw, lateral aspect. 1/7. (After Capellini.)

Halicore Illiger. Premaxillary with a pair of stout incisors. Cheek teeth: $\frac{5\text{-}6}{4\text{-}5}$, single rooted, small, peg-shaped. Recent.

Rhytina Illiger. Cheek teeth absent. A horny masticatory plate present in oral cavity. About the year 1768 *R. stelleri*, the Steller's sea-cow, was entirely exterminated.

Order X. PRIMATES. Anthropoid Mammals.[1]

Under the term Primates, Linnaeus included Man, the apes, the lemurs and the bats. The last-named animals have been removed from this order, and there remains a natural group of mammals closely allied to each other in anatomical respects, even though the terminal members in the series (Man and the lemur) apparently have but few characters in common. Three suborders of Primates are recognised, *Prosimia*, *Anthropoidea* and *Bimana*.

[1] *Brown, Al.*, On some Points in the Phylogeny of the Primates. Proc. Acad. Nat. Sci. Philad., 1901.—*Cope, E. D.*, The Lemuroidea and the Insectivora of the Eocene of North America. Amer. Naturalist, 1885.—*Filhol, H.*, Ann. Sci. Géol., vols. v., viii., xiv., xvii.—*Gervais, P.*, Zoologie et paléontologie générales, 1876, vol. ii.—*Granger, W., and Gregory, W. K.*, Revision of Notharctus. Bull. Amer. Mus. Nat. Hist., New York, 1917.—*Gregory, W. K.*, Relationship of Notharctus. Bull. Geol. Soc. Amer., vol. 26, 1915. Phylogeny of recent and extinct Anthropoids. *Ibid.*, 1916. On the structure and relations of Notharctus. Mem. Amer. Mus. Nat. Hist., 1920.—*Leche, W.*, Untersuchungen über das Zahnsystem lebender und fossiler Halbaffen. Festschrift für Gegenbaur, Leipzig, 1896.—*Osborn, H. F.*, American Eocene Primates. Bull. Amer. Mus. Nat. Hist., 1902.—*Schlosser, M.*, Die Affen, Lemuren, Chiropteren, etc., des europaischen Tertiars. Beitr. zur Paläont. Öst.-Ungar., 1887, vol. 6.—Beitrag zur Osteologie von Necrolemur und zur Stammesgeschichte der Primaten. Neues Jahrb. für Mineral., 1908. Festband.—*Stehlin, H. G.*, Säugetiere des schweiz. Eocäns. VII. Abh. Schweiz. Paläont. Ges., 1912, 1916.—*Winge, Herluf*, Jordfundne og nu levende Aber (Primates) fra Lagoa Santa, Brasilien. E. Museo Lundii. Copenhagen, 1895.—*Wortman, J. L.*, Studies of Eocene Mammalia in the Marsh Collection. Part ii. Primates. Amer. Journ. Sci., 1903 and 1904.

Suborder A. PROSIMIA (LEMUROIDEA). Lemurs.

Plantigrade, usually pentadactyl, frugivorous or omnivorous arboreal quadrupeds, with opposable hallux. All digits have nails except digit II. of the manus. Dentition frequently complete. Superior molars bunolophodont, quadritubercular, or tritubercular. Premolars less complex than molars. Inferior molars quadritubercular or quinquetubercular. Nasal bones and muzzle elongated. Orbits posteriorly limited by bone, but not separated by a wall from the temporal fossa. Lachrymal foramen lying outside the orbit. Brain slightly convoluted, the cerebellum not covered by the cerebral hemispheres. Mammae pectoral or abdominal.

The lemurs are inhabitants of Madagascar especially, but are likewise found in tropical Africa and southern Asia. They are distinguished from the true apes by the smaller, less convoluted brain, by the large orbit posteriorly limited by a bony bar but not by a wall of the temporal fossa, by the lachrymal foramen lying outside the orbit, by the partially clawed digits, by the opposable inner digit on the manus and pes, which is always well developed, by the hairy covering of the face, the bicornuate uterus, and usually abdominal mammae. The placenta is diffuse or bell-shaped; a decidua is absent.

In many respects the skeleton of the lemur is more primitive than that of the apes, and recalls that of the *Insectivora*, *Creodontia* and modern *Carnivora*. The hind-limbs are always longer than those in front, co-ossification never occurs in the carpus and tarsus, and as a rule a centrale is present in the former. Calcaneum and naviculare are frequently elongated. The dentition is either continuous or the series may be interrupted by a diastema. The superior molars are either tritubercular or more frequently quadritubercular in structure, and the protocone assumes a V-shaped form; it is joined to the external cusps by the two diverging sides, so that the dental crown is trigonodont, that is, bunolophodont. If it at all enters into the composition of the tooth, the hypocone always remains inferior in size to the protocone. A strong basal cingulum is generally present, which sometimes forms an inner wall. Small intermediate conules also occur in various genera. As in the ungulates, the talon on the inferior molars consists of a bicuspid posterior portion, which in length and breadth does not fall below the anterior half. The latter frequently exhibits the three primitive cones, although the protocone is far less robust than the two others and often disappears completely; hence the dental crown of the inferior molars consists of two pairs of opposite or somewhat alternating tubercles, which are usually united by transverse or oblique ridges. The premolars are always less complex than the molars. While in the fossil forms three incisors, often four premolars, and three molars are developed, in existing lemurs never more than three premolars and two incisors are present above and below, and the first premolar in the mandible exhibits a most marked and stout structure; it assumes the form and function of a true canine, yet does not like this come in contact with the normally formed superior canine, but like a true premolar it is inserted between the latter canine and the first superior premolar. The peculiar inferior canine immediately follows the incisors and also agrees with them in form and function, as in the ruminants. The superior incisors are small, curved, conical, or spatulate, those below, however, being unusually slender, awl-shaped, much elongated, and close together.

The *Prosimia* are separated into six families: *Adapidae*, *Anaptomorphidae*, *Tarsiidae*, *Lemuridae*, *Chiromyidae* and *Galeopithecidae*. The first two occur only in the older Tertiary; Europe and North America. Several genera of the true lemurs are known from the Pleistocene of Madagascar. The last two families belong exclusively to the Recent.

Family 1. **Adapidae** Trouessart.

Dental formula: $\frac{2.1.4.3.}{2.1.4.3.}$. *Dental series continuous above and below. Incisors and canines normal. Superior molars tri- or quadritubercular, protocone large, V-shaped; hypocone small. Lachrymal foramen at the anterior border of the orbit. Humerus with entepicondylar foramen. Tarsus not elongated.* Fossil in the Eocene; Europe and North America.

The skulls of *Adapis* (Fig. 355) and *Notharctus* are characterised by a high sagittal crest and relatively small orbits, beyond which the facial portion is much constricted. The elongated muzzle with its long narrow nasal bones, the completely closed orbits, and the position of the lachrymal foramen are all distinctive of the lemurs. In many forms, however, the two rami of the mandible are anchylosed at the symphysis, while the ascending branch is characterised by considerable breadth and depth, and there is usually a process on the posterior border. Two or three small foramina are found below the anterior premolar. The large greatly inflated auditory bullae, which diminish anteriorly, also recall the *Lemuridae*. In the anterior portion, at least, the dentition approaches more nearly that of the true apes, especially the American apes, than that of the lemurs. In other respects it is characterised on the whole by indifferent primitive characters. Although they possess a quadritubercular crown, the tritubercular type may still be distinctly recognised in the superior molars, for the small postero-internal column (hypocone) always appears as an accessory tubercle. The quinquetubercular or quadritubercular inferior molars show no marked differentiation, and could as well pertain to primitive ungulates or creodonts as to the lemurs. In comparison with those of apes and lemurs, the premolars are fully developed and, with the exception of the most anterior, are single rooted and monocuspid, with an internal tubercle above and a talon below. In the mandible, the fourth premolar is often like the first molar, while the last superior premolar reaches at the most the tritubercular stage. The posterior milk cheek tooth in both jaws agrees with the anterior true molar. The canines above and below are conical, tapering, somewhat decurved, and have the same structure as in all primitive ungulates, insectivores, carnivores, and apes, but not as in the existing lemurs. The development of a third pair of incisors in *Hyopsodus*, however, also here

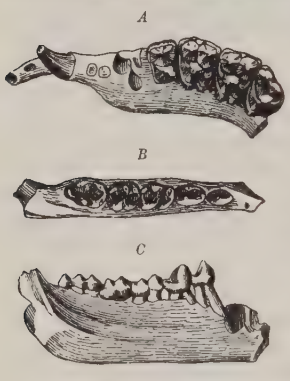


Fig. 354.

A, *Pelycodus tutus* Cope. Lower Eocene (Wasatch beds), Wyoming. Left upper jaw, palatal aspect. 1/1. *B*, *C*, *Pelycodus frugivorus* Cope. *Ibid.* Lower jaw, upper and outer aspects. 1/1. (After Cope.)

emphasises the primitive structure of the dentition. In *Adapis*, the permanent dentition has but two incisor teeth, while the milk dentition often has three. The bones of the skeleton at present known agree best with those of the *Lemuridae*.

The genera pertaining to this family were embraced by Cope in the *Mesodonta*, but he erroneously united with these the genus *Anaptomorphus*, while Filhol erected the group *Pachylemuridae* for the genus *Adapis*. Both authors failed to give diagnoses for the divisions which they established.

Pelycodus Cope (Fig. 354). Dental formula: $\frac{2.1.4.3.}{2.1.4.3.}$. Superior molars

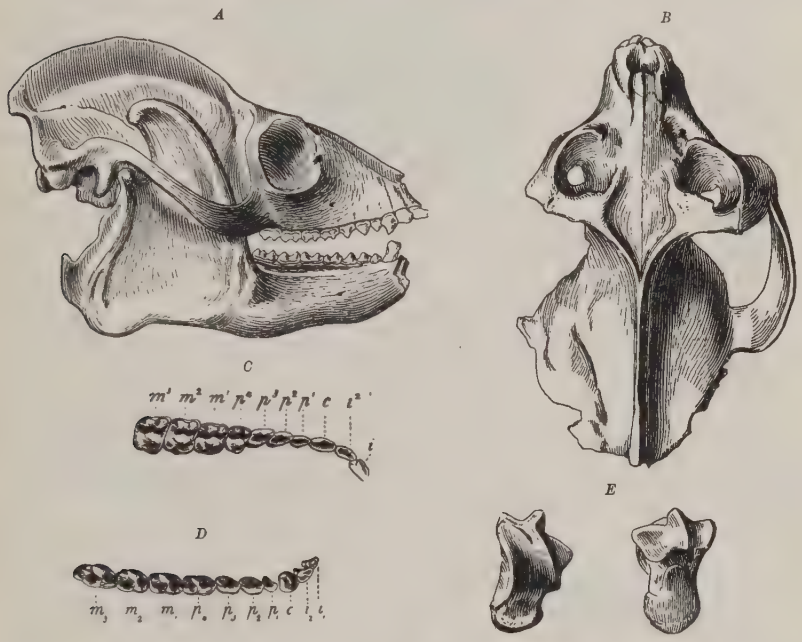


FIG. 355.

Adapis parisiensis Cuvier. Upper Eocene (Phosphorites), Quercy. *A*, Skull with lower jaw from right side; *B*, from above. *C*, Grinding surface of upper teeth; *D*, of lower teeth. 2/3. *E*, Astragalus, anterior and posterior aspects. 1/1.

quadrate, with two pyramidal external tubercles, a stout V-shaped protocone and a weak hypocone; intermediate tubercles very weak or wanting. Third molar trigonodont, hypocone suppressed. Inferior molars with two pairs of blunt opposite cusps and often with one weak single anterior tubercle. Third molar with a cusp on the posterior border. The anterior half of the molar is deeper than the posterior half. Premolars simple in structure. Astragalus with tibial articular surface scarcely furrowed. Terminal phalanges claw-shaped. Lower Eocene (Wasatch beds); Wyoming. *P. tutus* and *frugivorus* Cope.

Cryptopithecus Schlosser. Only mandibles known. Fourth premolar short but molariform. Molars with two deep anterior tubercles and low tricuspid

talon. Third molar smaller than second. Upper Eocene; Swabian Bohnerz. *C. siderolithicus* Schlosser. Oligocene (Brown Coal), near Darmstadt.

Pronycticebus Grandidier. First and second upper premolars very small, third and fourth bitubercular. Molars tritubercular. Eocene (Phosphorites); Quercy. *P. gaudryi* Grand.

Periconodon Stehlin. Third upper premolar with one tubercle. Upper molars with one slight intermediate tubercle and two strong inner basal tubercles. Eocene (Bohnerz); Egerkingen.

Aphanolemur Granger and Gregory. Skull much resembling that of *Adapis*. Middle Eocene (Bridger beds); Wyoming.

Adapis Cuvier (*Palaeolemur* Filhol; *Aphelotherium*, *Leptadapis* Gervais) (Fig. 355). Dental formula: $\frac{2.1.4.3.}{2.1.4.3.}$. Dental series continuous. Superior molars with two pyramidal external tubercles, a V-shaped protocone and smaller conical hypocone; sometimes, also, with a diminutive intermediate conule on the anterior border. Fourth upper premolar tritubercular, the three anterior premolars compressed, monocuspid, with strong internal talon-like basal cingulum. Upper canine laterally compressed, pointed, with trenchant anterior and posterior margins, more or less strongly protruding. Upper incisors small, spatulate, with short crown. Inferior incisors small, directed obliquely forward, chisel-shaped. Inferior canine stout, with truncated apex. The three anterior premolars compressed, the first two with a single root, the third two-rooted. Fourth premolar and molars with two pairs of cusps obliquely opposite, united by a ridge. Upper Eocene; Gypsum of Montmartre, Phosphorites of Quercy, and freshwater marls of St. Hippolyte de Caton, Gard. *A. parisiensis* Cuvier, *A. magnus* Filhol. Latter species also in Upper Eocene, Hordwell, Hants.

Fig. 356.

Caenopithecus lemuroides Rütimeyer. Eocene (Bohnerz), Egerkingen. Three upper molars. *A*, Outer aspect. *B*, Grinding surface. 1/1. (After Rütimeyer.)

Notharctus Leidy (*Tomitherium* Cope; *Thinolestes*, *Limnotherium* and *Telmatolestes* Marsh). Inferior molars with low crown, broad talon, and rugose enamel. Eocene (Wind River beds); North America. *N. venticolus* Osborn. Bridger beds. *N. rostratus* Cope.

Caenopithecus Rütimeyer (Fig. 356). The only superior molars known have quadrate crowns and consist of two blunt pyramidal external cusps, a V-shaped or subcrescentic internal tubercle, another very small postero-internal conule close to the basal cingulum, and a diminutive intermediate conule on the anterior border. Third molar only a little less inferior in size to the penultimate molar. *C. lemuroides* Rütimeyer. Bohnerz; Egerkingen.

Family 2. **Anaptomorphidae** Cope.

Dental formula: $\frac{3\text{-}2.1.\ 3.\ 3.}{2\text{-}1.1.2\text{-}4.3.}$. *Incisor and canine teeth normal, but relatively small. Inferior premolars short and stout. Superior molars tritubercular or quadritubercular, with small intermediate cusps. Skull brachycephalic; lachrymal foramen lying in front of the very large orbit. Rami of the mandible not anchylosed at the symphysis.* Eocene; Europe and North America.

Wortman united the *Anaptomorphidae* with the *Tarsiidae* in the group *Palaeopithecini*, and these again with the *Arctopithecini-Hapale* on the one hand and the *Neopithecini-Adapidae, Cebidae, Cercopithecidae, Simiidae* and *Hominidae* on the other, in the suborder *Anthropoidea* as opposed to the other *Primates*—*Cheiromyoidea* and *Lemuroidea*. In any case the *Anaptomorphidae* are closely related to the *Tarsiidae*.

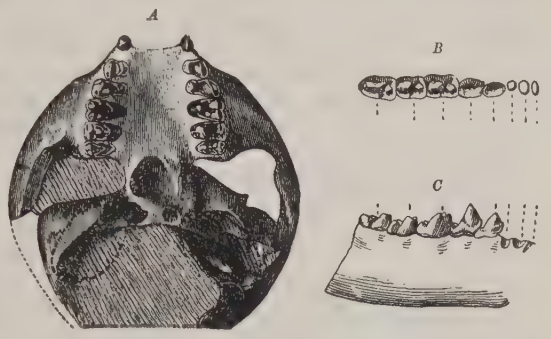


Fig. 357.

Anaptomorphus homunculus Cope. Lower Eocene (Wasatch beds), Wyoming. *A*, Skull, palatal aspect. 2/1. (After Cope.) *B*, *C*, Lower jaw. 3/2. (After Osborn.)

Anaptomorphus Cope (*Microchoerus* Leidy *partim*) (Fig. 357). Dental formula: $\frac{2.1.\ 2.\ 3.}{2.1.3\text{-}2.3.}$ Superior incisors unknown; canine small, peg-shaped, separated by a short interval from the two short premolars. Molars much broader than long, tritubercular, the internal cone V-shaped. Inferior molars very broad, with two pairs of opposite tubercles and an antero-internal cusp. Skull short, nearly as broad as long. The posterior border of the large orbit is chiefly formed by the postorbital process of the frontal bone. Eocene; Wasatch to Uinta beds, North America.

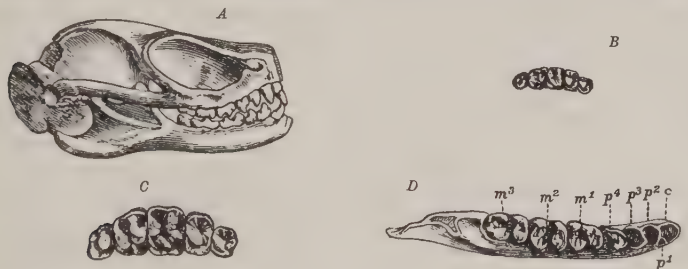


Fig. 358.

Necrolemur antiquus Filhol. Upper Eocene (Phosphorites), Quercy. *A*, Skull and lower jaw, right lateral aspect. 1/1. (After Filhol.) *B*, *C*, Upper cheek teeth, natural size and enlarged. (After Lydekker.) *D*, Lower jaw from above. 2/1.

Omomys Leidy (*Palaeacodon, Hemiacodon* and *Euryacodon* Marsh). Premolars: 3/3. Superior molars very broad, tritubercular; inferior molars nearly always with anterior cone (paraconid). Eocene (Bridger beds); North America.

Washakius Leidy. Inferior molars with four cones in the anterior half; first and second superior molars with small second internal cusp (hypocone). Eocene (Bridger beds); North America.

Necrolemur Filhol (Fig. 358). Dental formula: $\frac{3.1.\ 3.\ 3.}{1.1.(4)3.3.}$ Dental

series continuous. Superior molars quadrate, externally with two pyramidal tubercles, internally with two V-shaped cusps and two small intermediate conules; third molar smaller, trigonodont, with but one internal cusp. Premolars tritubercular. Inferior molars quadrate, with two pairs of cones and one weak arcuate conule on the anterior border; third molar with talonid. Between the canine and second premolar is found a diminutive denticle, pushed out of the series, that evidently represents the first premolar, which was supposed to have disappeared. Calcaneum and navicular elongated as in *Tarsius* and *Chirogaleus*. Femur and tibia as in *Tarsius*. Upper Eocene, Phosphorites; Quercy. *N. antiquus*, *N. edwardsi* Filhol. Bohnerz; Egerkingen and Mauremont. *N. cartieri* Rütimeyer.

Microchoerus Wood. Upper Eocene; Hordwell, England. Only upper jaws known.

Family 3. **Lemuridae** Gray.[1]

This family, which is restricted to Madagascar, is here considered only in connection with the following fossil genera, of which *Megaladapis* is especially distinguished by its gigantic size. The extinct forms further differ from the existing lemurs in the more normal structure of the incisors.

Megaladapis Forsyth Major (*Palaeolemur*, *Mesoadapis* Lorenz von Liburnau). Dental formula: $\frac{0.1.3.3.}{2.1.3.3.}$. Skull long and narrow, with long nasal bones, large obliquely placed prominent orbits and strong parietal and occipital crests. Superior canine large; superior premolars with one external and one internal tubercle, rounded trigonodont in cross-section like the superior tritubercular molars. Inferior molars with two alternating external and internal tubercles joined by a ridge. Third molar with third lobe; fourth premolar less complex than the molars. Brain remarkably small, with weak olfactory lobes and distinct cerebellum. Femur like that of *Pterodicticus*. Early Pleistocene; Madagascar. *M. madagascariensis* and *insignis*, Forsyth Major. The latter species is the largest of all known Primates, with skull over 30 centimetres in length. According to Forsyth Major, the nearest existing allies are *Lepidolemur* and the *Indrisinae*.

Peloriadapis (*Thaumastolemur* Filhol) and *Palaeochirogaleus* Grandidier are the size of man, but are very imperfectly known.

Hadropithecus (*Pithecodon*) Lorenz von Liburnau. Two incisors, three premolars and three molars. Anterior molars trenchant; fourth premolar molariform.

Nesopithecus Forsyth Major (*Lophiolemur* Filhol; *Globilemur* Forsyth Major; *Bradylemur* Grandidier; *Protoindris* Lorenz von Liburnau). Dental formula: $\frac{2.1.3.3.}{2.0.3.3.}$. Cranium large, without prominent parietal crest. Eyes directed forward; orbits without septum; distinct tympanic ring, large osseous bullae. Large very complicated cerebrum tapering toward the front; small

[1] *Grandidier, G.*, Les Lémuriens disparus. Nouvelles Arch. du Muséum Paris, 1905.—*Forsyth Major, C. I.*, Summary of the present knowledge of extinct Primates from Madagascar. Geol. Mag., 1900.—*Lorenz von Liburnau, L.*, Ausgestorbene Primaten von Madagaskar. Denkschr. Akad. Wiss. Wien, math.-naturw. Cl., vol. lxx., 1900. Hadropithecus. *Ibid.*, vol. lxxii., 1901. Megaladapis. *Ibid.*, vol. lxxvii., 1905.—*Standing, H. F.*, Subfossil Primates from Madagascar. Trans. Zool. Soc., vol. xviii., 1908.

uncovered cerebellum. Inferior incisors nearly vertical; superior canine immediately in front of the first lower premolar. Premolars trenchant. Molars with cusps united into a ridge. Humerus with entepicondylar foramen. *N. roberti* Forsyth Major, possibly stands near the origin of the Cercopithecines.

Palaeopropithecus Grandidier. Dental formula: $\frac{2.1.2.3.}{2.0.2.3.}$. Cranium depressed, with postorbital constriction.

Mesopropithecus Standing. Dental formula as in *Palaeopropithecus*, but cranium rounded and relatively larger.

Suborder B. ANTHROPOIDEA Mivart (*Simiida*). Apes.[1]

Plantigrade, land or arboreal quadrupeds, walking either on the sole or external border of the foot, with opposable pollex and hallux. Except in the Hapalidae, all terminal phalanges flattened and provided with nails. Dentition nearly complete, with but two pairs of incisor teeth and a small diastema. Cheek teeth bunodont, as a rule quadritubercular above and below; superior molars sometimes tritubercular. Orbits directed forward, separated posteriorly from the temporal fossa by a bony wall. Lachrymal foramen lying within the orbit. Brain large, strongly convoluted. Two pectoral mammae.

The apes chiefly inhabit the tropical regions of Africa, Asia and America. A single species lives on the Rock of Gibraltar. Fossil apes first appear in the Oligocene of Egypt, are known from the Middle Miocene of Europe and are found sparingly in the later Miocene, Pliocene and Pleistocene of Europe, southern Asia and northern Africa. South America also furnishes Tertiary and Pleistocene forms, which include the existing *Cebidae* and *Hapalidae* (*Platyrhini*) of that region.

In size and external appearance the apes show extraordinary diversity. While the lowest and smallest forms still closely resemble the lemurs, in the structure of the entire body the highest and largest types are anthropoid.

The skull has a very spacious brain-cavity; the deeply convoluted hemispheres of the cerebrum almost entirely cover the cerebellum, and in size and abundance of convolutions are inferior only to those in man. The large subcircular orbits are directed forward, and posteriorly are separated from the temporal fossa by a bony plate formed by the ascending portion of the

[1] *Ameghino, F.*, Les Formations sédimentaires de Patagonie. Anal. Museo Nac. Buenos Aires, 1906.—*Beyrich, C.*, Über Semnopithecus pentelicus. Abh. Berlin Akad., 1860.—*Boule, M.*, Singes fossiles de l'Inde. L'Anthropologie, vol. xxvi., 1915.—*Branco, W.*, Die menschenähnlichen Zähne aus den Bohnerzen der schwäbischen Alb. Jahresh. Ver. Vaterl. Naturkunde in Württemberg, 1898.—*Dubois, E.*, Über drei ausgestorbene Menschenaffen. N. Jahrb. für Mineral., 1897, vol. i.—*Gaudry, A.*, Le Dryopithèque. Mém. Soc. Géol. France. Palaeontol., 1890, vol. i.—*Harlé, Ed.*, Une Machoire de Dryopithèque. Bull. Soc. Géol. France, 1898.—Nouvelles pièces de Dryopithèque. *Ibid.*, 1899.—*Lydekker, R.*, Palaeontologia Indica, 10. ser. vol. iv. Siwalik Mammalia. Suppl. L. 1886.—*Pilgrim, G. E.*, New Siwalik Primates. Rec. Geol. Surv. India, vol. xlv., 1915.—*Ristori, G.*, Scimmie fossili italiane. Boll. Comitato Geol. Ital., 1890.—*Schlosser, M.*, Beitr. z. Kenntnis der Säugetiere aus den süddeutsch. Bohnerzen. Geol. u. Paläont. Abh., Jena, 1902.—Die neueste Literatur über die ausgestorbenen Anthropomorphen. Zool. Anzeig., 1900.—Die menschenähnlichen Zähne aus den Bohnerzen der schwäbischen Alb. Zool. Anz., 1901.—*Schwalbe, G.*, Oreopithecus. Zeitschr. f. Morph. u. Anthrop., vol. xix., 1915.—*Stromer, E.*, Wirbeltierreste aus dem Mittelpliocän des Natrontales (Ägypten). Zeitschr. Deutsch. Geol. Ges., 1913.—*Wagner, A.*, Abh. K. Bay. Akad., II. Cl., vol. iii. 1. Abth. vol. vii. 2. Abth. vol. viii. 1. Abth.—*Woodward, A. S.*, Dryopithecus. Quart. Journ. Geol. Soc., vol. lxx., 1914.

jugal. The lachrymal bone, as well as the lachrymal foramen, lies within the anterior margin of the orbit. The facial bones are only moderately elongated, are sometimes very short, and ascend abruptly backward. The nasal bones are short; the narial aperture is directed forward and is bounded above by the nasals, laterally and below by the premaxillaries. The frontals are anchylosed into a single bone; the large parietal bones meet at the sagittal suture and only exceptionally form a parietal crest. As a rule, the supra-orbital ridge is also but slightly developed. The mandible has a horizontal inferior margin, a high and usually broad ascending branch, and an obliquely inclined chin, in which the two anteriorly converging branches are co-ossified.

In front of the generally robust conical canine above, and posterior to it below, the dentition is interrupted by a small diastema. The stoutness of the canine is greater in the male than in the female. Only two chisel-shaped incisor teeth are constantly present on each side above and below. In all Old World apes, the superior molars have four, directly or obliquely opposite, obtuse, conical or angular tubercles, the hypocone being sometimes weaker than the protocone. In American apes, the protocone is sometimes entirely absent. The inferior molars have but two pairs of tubercles, which often are united by thin transverse ridges, yet frequently remain quite distinct. The third molar is characterised by an additional cusp on the posterior margin. The premolars above and below consist of a usually pointed external cusp and a stout but low internal tubercle. In the Old World apes there are two premolars present on each side above and below, but in the New World forms there are three premolars. In the milk dentition, the posterior cheek teeth are like the first true molar.

The vertebral column consists of seven cervical, eleven to fourteen dorsal, four to seven lumbar, five sacral, and an extremely variable number of caudal vertebrae. The individual vertebrae, as well as the remaining bones of the skeleton, agree essentially with those of man. In many South American apes, the tail attains three times the length of the body; in the Old World *Simiidae*, it is completely absent. The relative length of the anterior and posterior extremities varies extremely. In the *Cercopithecidae*, both are of moderate and approximately equal length; in *Hylobates* and *Ateles*, they are much elongated, while in most *Simiidae*, the anterior extremities are considerably longer than those behind. The humerus often has an entepicondylar foramen. The radius and ulna are separate, stout, and can be twisted round each other. The carpus is short and broad; its posterior border articulating with the forearm forms a convex curve; the carpals are all distinct, and, except in the Chimpanzee and Gorilla, a rather large centrale is present. The trapezium has a saddle-like articular surface for the opposable thumb, which, however, is frequently represented merely by a short vestige of the metacarpal, and is less movable than in man. The phalanges are convex on the dorsal side and flat on the plantar surface, the last phalanx being reduced distally, flattened and scarcely curved. The slender femur lacks a third trochanter; the tibia and fibula are well developed and touch each other only at their extremities. The astragalus has a convex, unfurrowed, tibial articular surface, and a lateral facet for articulation with the fibula. The calcaneum has a long tuberosity and is distinctly truncate below. The short but stout hallux is always opposable; hence the pes is fitted to assume the function of a hand.

The apes are divided into five families, the *Hapalidae*, *Cebidae*, *Parapithecidae*, *Cynopithecidae* and *Simiidae*. The last two belong to the Old World and are characterised by a narrow nasal septum with narial apertures directed forward (*Catarhini* Geoffroy). The two first-named families inhabit South America; their narial openings are directed laterally (*Platyrhini* Geoffroy). Fossil remains of all families also exist, yet only in moderate numbers and usually in very imperfect preservation.

Family 1. **Hapalidae** Wagner. Marmosets.

Dental formula: $\frac{2.1.3.2.}{2.1.3.2.}$. *The two superior molars tritubercular, internal tubercle* V*-shaped. Superior premolars broader than long, with pointed external and internal cusps. Inferior molars quadritubercular, the posterior pair of cusps lower than the anterior ones. Canine strongly protuberant. Skull roundish; orbits relatively small. With the exception of the hallux, all digits on both extremities furnished with claws. Tail longer than the entire body.*

The single genus *Hapale* Illiger inhabits tropical South America. It was divided by Geoffroy into two subgenera *Jacchus* and *Midas*. Lund found two fossil species of the former in Brazilian caves.

Family 2. **Cebidae** Swainson.

Dental formula: $\frac{2.1.3.3.}{2.1.3.3.}$. *Superior and inferior molars quadritubercular. Premolars bicuspid. All digits with nails. Tail long.*

Living in tropical South America and Central America. Fossil in the Tertiary and Pleistocene of South America.

Homunculus Ameghino (*Ecphantodon* Mercerat) (Fig. 359). Diastema very small. Canine but slightly protuberant, with basal conule on the posterior side. The single-rooted premolars with low external cusp and two internal conules developed from the basal cingulum. Molars subquadrate, with two pairs of tubercles united by oblique transverse ridges; first molar somewhat smaller than the two posterior cheek teeth. Humerus with entepicondylar foramen. Upper Miocene; Santa Cruz, Patagonia. *H. patagonicus* Ameghino.

Fig. 359.

Homunculus patagonicus Ameghino. Upper Miocene (Santa Cruz beds), Patagonia. Skull, oblique left lateral aspect. $^1/_1$. (After Ameghino.)

? *Anthropops* Ameghino; ? *Homocentrus* and *Eudiastatus* Ameghino. Santa Cruz. *Pitheculus* Ameghino. Colpodon beds; Patagonia. *Protopithecus* Lund. Pleistocene; Brazil. These are based on very incomplete remains.

Cebus Erxleben, *Mycetes* Illiger (*Stentor* Geoffroy), *Callithrix* Erxleben. Living in South America. Fossil in bone caves of Brazil.

Family 3. **Parapithecidae** Schlosser.

Dental formula : $\frac{2.1.2.3.}{2.1.2.3.}$. *Incisors small, canine little longer and somewhat inclined forwards. First premolar simple, without inner tubercles. Molars consisting of two pairs of stout tubercles with a small tubercle behind ; these tubercles alternating in* M_1 *and* M_3, *but opposed in* M_2. *Front half of molar somewhat higher than hinder half. Mandible low, the rami strongly divergent, with weak symphysis.*

FIG. 360.

Parapithecus fraasi Schlosser. Oligocene, Fayum, Egypt. Lower jaw from above. $^1/_1$. (After Schlosser.)

In the form and characters of the teeth and jaw, and in the size of the animal, the *Parapithecidae* are intermediate between the *Anaptomorphidae* and *Tarsiidae* and *Pliopithecus* of the family *Simiidae*.

Parapithecus Schlosser (Fig. 360). Oligocene, Fayum, Egypt. *P. fraasi* Schlosser.

Moeripithecus Schlosser. Oligocene, Fayum. Known only by second and third lower molars. *M. markgrafi* Schlosser.

Family 4. **Cynopithecidae** Gill.

Dental formula : $\frac{2.1.2.3.}{2.1.2.3.}$. *Molars quadritubercular above and below, the external and internal pairs at times separated by a deep longitudinal furrow, at times united by a transverse crest. Third inferior molar with talon. Premolars bicuspid. Muzzle produced, frequently elongate. Extremities plantigrade. Tail usually long. Ischiatic callosities present.*

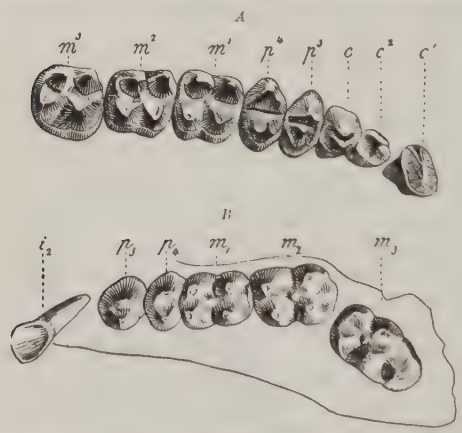


FIG. 361.

Oreopithecus bambolii Gervais. Miocene, Tuscany. *A*, Upper teeth from Casteani. $^1/_1$. (After Ristori.) *B*, Lower teeth from Monte Bamboli. $^1/_1$. (After Gervais.)

To the *Cynopithecidae* belong the Old World baboons, macaque, the long-tailed monkey, the short-tailed and the slender monkeys. These step with the whole sole of the foot, nearly always go on all four extremities, and generally possess a more or less elongate tail, as well as cheek-pouches and ischiatic callosities. The fossil forms occurring in the Pliocene and Pleistocene of Europe and Asia are rather closely allied to existing genera.

Oreopithecus Gervais (Fig. 361). Canines weak, above and below. Superior molars with two pairs of opposite conical tubercles separated by a

median longitudinal furrow, and with a strong basal cingulum. Third molar scarcely smaller than the second. Superior premolars with high external cusp and strong internal tubercle. Inferior molars narrower than those above, with two pairs of tubercles and a single cusp on the posterior border, which in the third molar is developed into a strong talonid. Upper Miocene; Tuscany. *O. bambolii* Gervais. Also Bessarabia.

Simopithecus Andrews. Lower Pleistocene, British East Africa. *S. oswaldi* Andr.

Cynocephalus Lacépède. Baboon. Living in Africa and Arabia. Fossil in the Siwalik deposits of India. *C.* (*Semnopithecus*) *subhimalayanus* Meyer sp. *C. falconeri* Lydekker. Also in the cavern deposits, Madras, and Pleistocene or later deposits in British East Africa and Algeria.

Semnopithecus Cuvier. Living in south-eastern Asia. Fossil in the Pliocene of Montpellier, France; Messina, Sicily; and Casino, Tuscany. S. *monspessulanus* Gervais. Siwalik deposits; India. *S. palaeindicus* Lydekker. Pleistocene; India. *S. entellus* Duf.

Mesopithecus Wagner (Fig. 362). Skull and dentition as in *Semnopithecus*, the skeleton, however, more robust and agreeing better with *Macacus*. The males have considerably stouter canines than the females. *Mesopithecus pentelici* Wagner, from the Lower Pliocene of Pikermi, near Athens, is the most abundant and the most completely known fossil monkey. It occurs also at Veles (Macedonia), Baltavár (Hungary), Tiraspol (S. Russia), and Maragha (Persia).

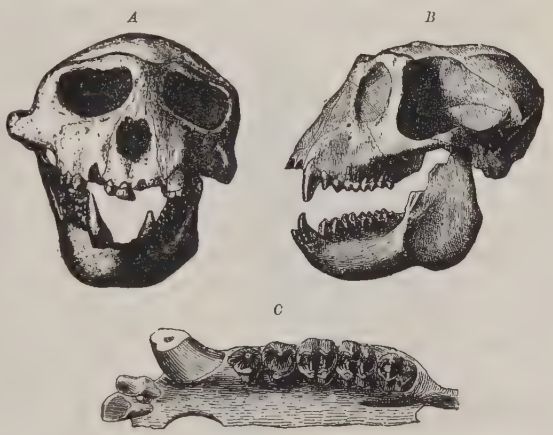


FIG. 362.

Mesopithecus pentelici Wagner. Lower Pliocene, Pikermi, Greece. *A*, *B*, Skull and lower jaw of male, anterior and left lateral aspects. 2/5. (After Gaudry.) *C*, Left upper jaw, palatal aspect. 1/1.

Dolichopithecus Depéret. Like *Semnopithecus*, with much elongated muzzle and shorter and more robust extremities. Pliocene; Perpignan. *D. ruscinensis* Depéret.

Macacus Lacépède (*Inuus* Geoffroy; *Aulaxinus* Cocchi). Superior molars low, quadrate, with two opposite pairs of obtuse conical or angular tubercles, at times separated by a median longitudinal furrow, at times united by a transverse crest. Premolars with external and internal cusp. Inferior molars like those above, but narrower; third premolar with stout talon. In the males canine powerful, rather strongly protuberant. *M.* (*Inuus*) *ecaudatus* Geoffroy is the only ape living on the Rock of Gibraltar in Europe, and in northern Africa. The remaining species of the genus *Macacus* have a wide distribution in southern and eastern Asia, and in part inhabit the highland regions of Tibet, the Himalayas and of Japan. *M. priscus* Gervais from

the Pliocene of Montpellier, and *M. sivalensis* Lydekker, from the Siwalik deposits, India, are the oldest fossil representatives of this genus. A mandible, as well as various isolated teeth (*Aulaxinus florentinus* Cocchi) from the Pliocene of Val d'Arno, was referred by Ristori to *Inuus* (*Macacus*). A well-preserved palate of *M.* (*Inuus*) *suevicus* was discovered by Hedinger in Heppenloch, near Kirchheim, Württemberg. In a rock-fissure of Montsanes, Haute-Garonne, Harlé found a fragment of a lower jaw of *Macacus* associated with Pleistocene mammals. Several jaws of *Macacus* were found by Forsyth Major near Cape Faro, Sardinia, and one lower jaw is known from Csarnota, Hungary. *M. pliocenus* Owen is represented by one molar from Grays, Essex, and the distal end of a humerus is known from the Forest Bed, Norfolk. *Macacus trarensis* Pomel and *M. proinuus* are from the Pleistocene, Algiers.

Family 5. **Simiidae.** Anthropoid Apes.

(*Anthropomorphidae* Ameghino.)

Dental formula : $\frac{2.1.2.3.}{2.1\ 2.3.}$. *Superior and inferior molars quadritubercular, the internal cusps alternating with the external ones ; the first internal tubercle of the superior molars always united with the external cusp. The last inferior molar either without or with a very weak talon. Premolars shorter than long, bicuspid. Canine larger than second incisor. Skull with sagittal and occipital crests or with supratemporal ridge. Anterior extremities longer than those behind. Gait usually upright. Tail absent. Ischiatic callosities present only in Hylobates.*

In their entire skeletal structure, the anthropoid apes approach nearest to Man, and are distinguished from the remaining apes by their highly developed brain, the ability to walk upright, not on the sole of the foot, as in Man, but on the external lateral margin ; further by the more or less prominent parietal and occipital crests, the high spinous processes of the cervical vertebrae, and the absence of a tail. The dentition also approximates to that of Man by the truncation of the cusps on the molars and by the disappearance of the talon on the last inferior cheek tooth ; it is distinguished from that in Man by the stronger development of the canines.

Fig. 363.

Propliopithecus haeckeli Schlosser. Oligocene, Fayum, Egypt. Lower jaw, outer aspect, and grinding surface of teeth. 1/1. (After Schlosser.)

Fig. 364.

Pliopithecus antiquus Blainv. sp. Upper Miocene, Steiermark. Left upper jaw, palatal aspect. 1/1.

Propliopithecus Schlosser (Fig. 363). Lower jaw high, the horizontal ramus with parallel borders. Incisors and canines small and upright.

Premolars simple, the hinder with inner tubercles. Molars low, with small hinder tubercle. Oligocene, Fayum, Egypt. *P. haeckeli* Schlosser.

Pliopithecus Gervais (*Protopithecus* Lartet *non* Lund) (Figs. 364, 365). Founded on a mandible. Incisors narrow, rather long. Canine stout, but not so high as incisor teeth. Cheek teeth low, compressed; anterior premolar monocuspid, posterior bicuspid. Inferior molars with two pairs of obliquely arranged obtuse conical tubercles and one weak single conule on the posterior margin, which in the third molar is developed into a talon-like basal cingulum. Middle and Upper Miocene; Sansan (Gers), Grive-St.-Alban (Isère) and Orleans. Lignite; Elgg, Switzerland, and Göriach, Styria; in the Bavarian Dinotherium sand, and near Oppel, Silesia. In size and dental structure

FIG. 365.

Pliopithecus antiquus Blainv. sp. Middle Miocene, Sansan (Gers). Lower jaw from above. 1/1. (After Blainville.)

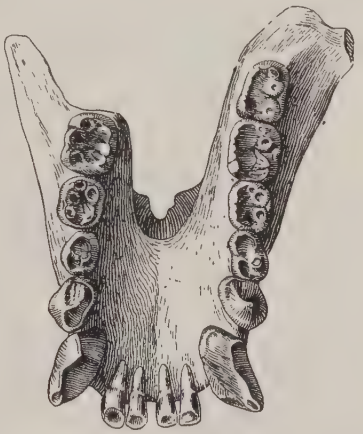


FIG. 366.

Dryopithecus fontani Lartet. Middle Miocene, St. Gaudens (Haute-Garonne). Lower jaw from above. 3/4. (After Gaudry.)

P. antiquus Blainville sp. (= *P. platyodon* Biedermann) approaches the existing gibbon (*Hylobates*) of southern India.

Palaeopithecus Lydekker. Only upper jaw known. Lower Pliocene; Siwalik deposits, Zobi, Punjab. Closely approximating the chimpanzee in size. The two premolars relatively small, short and broad. Molars rhomboid quadritubercular, smooth, anthropoid. Diastema between the stout canine and the incisors. *P. sivalensis* Lydekker.

Sivapithecus Pilgrim. Lower fourth premolar small, lower molars scarcely longer than broad, with almost smooth tubercles. Upper molars very broad. Lower and Middle Siwalik deposits. *S. indicus* Pilgrim.

Dryopithecus Lartet (*Paidopithex* Pohlig; *Pliohylobates* Dubois) (Fig. 366). Rami of mandible deep, nearly parallel, with weak incisors inclined forward and stout canine. Third premolar large, deep, monocuspid, with internal basal cingulum. Fourth premolar longer than broad, with two cusps and a cup-shaped talon. Inferior molars with two low alternating external and internal tubercles, and a single posterior cusp on the third molar in place of a bicuspid talonid. Superior molars with two external and two subequal internal cusps, the internal being joined to the external tubercles by a ridge.

Geological and Geographical Distribution of the Primates.

	Africa.	Europe.	Asia.	North America.	South America.
Recent	Chimpanzee Gorilla Cynopithecidae Lemuridae Chiromyidae	Macacus	Gibbon Orang Utan Cynopithecidae Lemuridae Galeopithecidae		Platyrhini (Cebidae, Hapalidae)
Pleistocene	Macacus Cynocephalus Megaladapis Peloriadapis Hadropithecus Nesopithecus	Eoanthropus Macacus	Pithecanthropus Semnopithecus Cynocephalus		Cebus Callithrix Mycetes Protopithecus
Pliocene	Libypithecus	Macacus Dolichopithecus Semnopithecus Dryopithecus Anthropodus Mesopithecus	Troglodytes Simia Macacus Semnopithecus Cynocephalus Palaeopithecus Sivapithecus		
Miocene		Dryopithecus Pliopithecus Oreopithecus			Homunculus Anthropops ? Pitheculus Eliastatus ?
Oligocene	Propliopithecus Parapithecus Moeripithecus				
Eocene — Upper		Cryptopithecus Adapis Necrolemur Microchoerus Pronycticebus Periconodon		Omomys	
Eocene — Middle (Bridger Beds and Bohnerz of Switzerland)		Caenopithecus Necrolemur		Notharctus Anaptomorphus Omomys Hemiacodon Euryacodon Washakius Aphanolemur	
Eocene — Lower (Wasatch Beds)				Pelycodus Anaptomorphus	
Eocene — Lower (Puerco Beds)		Plesiadapis ? Protoadapis ?		Gen. indet. Extremities	

Upper surface of all molars strongly rugose. Humerus from St. Gaudens slender and much shorter than the femur from Eppelsheim, which is little thickened distally. Upper Miocene; St. Gaudens, Haute Garonne; Seo de Urgel, Lérida, Spain. *D. fontani* Lartet. Lower Pliocene; Eppelsheim, and Bohnerz of Salmendingen, Melchingen and Trochtelfingen. *D. rhenanus* Pohlig sp. *Dryopithecus* approximated the chimpanzee in size, and may be the common ancestor of the latter and the orang.

Anthropodus Schlosser. Inferior third molar much longer than broad, with low tubercles, large talon, and strongly rugose enamel. Lower Pliocene (Bohnerz), Salmendingen. *A. brancoi* Schlosser. There are some resemblances to *Pithecanthropus* and *Homo*.

Australopithecus Dart.[1] Immature skull with milk dentition, of uncertain geological age, from Taungs, Bechuanaland, S. Africa.

Suborder C. BIMANA. Man.[2]

(*Hominidae* Schlosser.)

Gait erect. Manus with opposable thumb. Pes plantigrade, hallux not opposable. All fingers and toes with smooth nails. Dentition: $\frac{2.1.2.3.}{2.1.2.3.}$ *Teeth in completely continuous series, without diastema; canines weak, not protuberant. Orbits shut off by a bony wall posteriorly. Roof of skull without sagittal crest. Brain large, with deep and very numerous convolutions.*

Pithecanthropus Dubois.[3] Cranial roof narrow, but little arched, dolichocephalic, with postorbital constriction. Third superior molar strongly reduced, with many rugosities, without distinct cusps. Femur long, slender, exactly fitted for an upright gait. *P. erectus* Dubois. Upper Pliocene or Lower Pleistocene; Trinil, Java.

[1] *Dart, R. A.*, Nature, vol. 115, 1925, p. 195.

[2] *Birkner, F.*, Die ältesten menschlichen Knochenreste. Beiträge zur Anthr. und Urgeschichte Bayerns, vol. 18, 1909.—*Boule, M.*, Les Grottes de Grimaldi. L'Anthrop., 1906.—Observation sur un silex taillé et sur la chronologie de M. Penck. L'Anthrop., 1908.—*Boule, M.*, L'Homme fossile de la Chapelle-aux-Saints. Annales Paléont., 1911-13—Les Hommes fossiles, ed. 2. Paris, 1923 (English translation by Ritchie. Edinburgh, 1924).—*Burkitt, M. C.*, Prehistory, ed. 2. Cambridge, 1925.—*Hrdlička, A.*, Early Man in South America. Smithson. Inst. Bureau Amer. Ethnol., Bull. 52, 1912.—Recent Discoveries attributed to Early Man in America. *Ibid.*, Bull. 66, 1918.—*Johnson, J. P.*, Prehistoric Period in South Africa, ed. 2. London, 1912.—*Keith, A.*, The Antiquity of Man, ed. 2. London, 1925.—*Klaatsch, H.*, Die neuesten Ergebnisse der Paläontologie des Menschens. Zeitschr. f. Ethnol., 1909.—*Kramberger, Gorjanovic*, Der diluviale Mensch von Krapina. Wiesbaden, 1906.—*Lehmann-Nitsche*, Nouvelles recherches sur la formation Pampéenne et l'homme fossile de la Rép. Argentine. Revista del Museo de La Plata, 1907, vol. 14.—*Macalister, R. A. S.*, Text-book of European Archaeology, vol. i. Cambridge, 1921.—*Obermaier, H.*, El Hombre fósil. Museo Nacional, Madrid, 1916 (English translation, New York, 1924).—*Obermaier, H.*, Les Restes humaines quaternaires. L'Anthr., 1905 and 1906.—Les Formations glaciaires des Alpes. L'Anthr., 1909.—Die Steingeräte des franz. Altpaläolithikums. Mitteil. Prähist. Komm. Kaiserl. Akad. Wien, 1908.—*Osborn, H. F.*, Men of the Old Stone Age. New York, 1915 (and later editions).—*Schmidt, R.*, Die diluviale Vorzeit Deutschlands. Stuttgart, 1912.—*Schoetensack, O.*, Der Unterkiefer des Homo heidelbergensis. Leipzig, 1908.—*Schwalbe, G.*, Der Neandertalschädel. Bonner Jahrb., 1901.—Zur Frage der Abstammung der Menschen. Zeitschr. f. Morph. u. Anthr., 1906.—*Sollas, W. J.*, Ancient Hunters, ed. 3. London, 1924.—*Verneau, R.*, Les Fossiles aux Baoussé Roussé. Un nouveau type humain. L'Anthr., 1902.—Les Grottes de Grimaldi. L'Anthr., 1906.—British Museum Guide to the Fossil Remains of Man, ed. 3. London, 1922.

[3] *Dubois, E., Pithecanthropus erectus*, eine menschenähnliche Übergangsform aus Java. Batavia, 1894.—*Schwalbe, G.*, Studien über Pithecanthropus. Zeitschrift für Morph. u. Anthr., 1899.

Only the skull-cap, a tooth and the femur of *Pithecanthropus* are known. As these specimens, however, are characteristic portions of the skeleton, they are quite sufficient to give an idea of the organisation of this animal. Notwithstanding the large size of the skull, the cranial roof has neither sagittal crest nor temporal ridge. Consequently, the superior canine and the inferior third premolar functioning with it were without doubt not much larger than the second incisor. This character alone would be sufficient to exclude *Pithecanthropus* from the *Simiidae* (*Anthropomorphidae*) and to bring it in close relation to the genus *Homo*. The form and structure of the third superior molar are likewise occasionally found in Man but never occur in the *Simiidae*. The remarkably long femur also can only be compared with that of Man, from which it differs only in the more circular cross-section of the shaft, and the weaker development of the condylar region. While many German anthropologists are inclined to look upon *Pithecanthropus* merely as a huge *Hylobates*, Turner, Topinard and Manouvrier lay stress upon its great similarity to Man. In the structure of the skull of *Pithecanthropus*, Schwalbe also finds profound differences from that in the *Simiidae* (Anthropomorphs). The question whether *Pithecanthropus* may be the direct ancestor of the genus *Homo*, however, cannot yet be answered with certainty, and the geological age of this form is not exactly known.

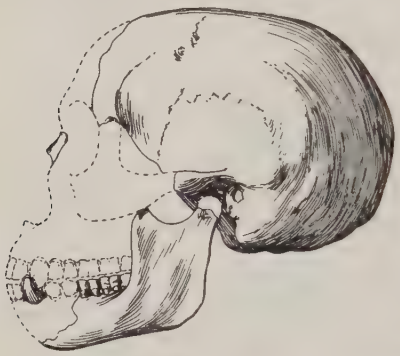


Fig. 367.

Eoanthropus dawsoni A. S. Woodward. Lowest Pleistocene gravel, Piltdown, Sussex. Restoration of skull and lower jaw. 1/4. (After A. S. Woodward.)

Eoanthropus A. S. Woodward[1] (Fig. 367). Cranium essentially human, without inflated brow-ridges, but depressed and wide at the occiput; cranial bones very thick, and consisting of fine spongy tissue. Size of brain at least 1300 cubic centimetres. Lower jaw with retreating bony chin, produced below into a thin flange as in apes. Canine teeth interlocking, the permanent lower canine shaped like the lower milk-canine of *Homo*; lower molars longer than broad, with a fifth tubercle at the hinder border. *E. dawsoni* A. S. Woodward, from an early Pleistocene gravel at Piltdown, near Uckfield, Sussex, associated with pre-Chellean flint implements. The type specimen consists of the greater part of a cranium, with isolated nasal bones, mandibular ramus, and canine tooth found close together in a gravel pit. A second specimen is represented by pieces of frontal and occipital bones and a lower molar tooth from another locality near Piltdown. Human teeth from the Tufa of Taubach, Weimar, may also belong to *Eoanthropus*.

Homo L. Linnæus placed Man in the order *Primates* and separated him only generically from the apes. In physical respects he is closely allied to

[1] *Dawson, C., and Woodward, A. S.*, Quart. Journ. Geol. Soc., vol. lxix. 1913; vol. lxx. 1914; vol. lxxi. 1915 (bone implement).—*Woodward, A. S., loc. cit.*, vol. lxxiii. 1917 (second skull). Guide to Fossil Remains of Man, British Museum, 3rd. ed., 1923.—*Osborn, H. F.*, Natural History (New York), vol. xxi., 1921, p. 577.

the apes, particularly to the *Simiidae* (Anthropomorphs); hence it is difficult to draw sharp anatomical distinctions between them. According to Huxley, the differences between the highest and lowest apes are far more marked than those separating Man and the anthropoid apes. The highly arched form of the very spacious skull-cap, the considerable preponderance of the cranial over the facial region, and the absence of a sagittal crest very clearly distinguish the head of Man from that of all higher apes, yet in these respects many South American forms approach very closely to Man. In size and weight the human brain very much surpasses that of all apes, but in anatomical structure, in the development of the cerebrum and the complexity of the convolutions, the same general plan prevails in apes and in Man. The fusion of the premaxillary with the maxillary, and the absence of a diastema, together with the relatively weak canine teeth, are unimportant characters. Compared with the produced muzzle (prognathous) of most apes, the face of man is abruptly sloping (orthognathous). With this facial structure is associated the almost vertical symphysial region of the mandible and a somewhat prominent bony chin.

In form, the lower jaw is horse-shoe shaped, and the two anchylosed rami enclose a much broader space for the tongue than in any apes. In the number and form of the teeth, the dentition agrees with that of the Old World apes; the canines, however, scarcely project beyond the continuous dental series, and the tubercles of the cheek teeth are more obtuse, broader and lower than in the apes. As a rule, the superior and inferior molars are quadritubercular. On the superior molars, however, the hypocone remains inferior in size to the protocone and is sometimes suppressed, in which case a tritubercular tooth results. In the inferior molars, the four principal cusps are frequently accompanied by a single conule on the posterior border. The single-rooted premolars are less complex and shorter than the molar teeth, and consist of an external and internal tubercle. In Australians, New Caledonians and negroes, a fourth molar sometimes appears, as in the orang, while in civilised races there is a noticeable tendency toward the suppression of the last molar (wisdom tooth). The double sigmoid curve in the spinal column, the considerable length and strong musculature of the limbs, the breadth of the shoulders and the proportionately short length of the arms are correlated with the upright gait. In mobility and capacity for adaptation, the human hand far surpasses the hand of apes. The thumb is strongly developed, opposable and very movable. The sole of the foot is horizontal. The metatarsals and tarsals form an arch, and the stout non-opposable hallux cannot be used in grasping, but merely aids in supporting the weight of the body.

Numerous authentic remains of fossil Man occur in the Pleistocene, where domestic animals are wanting, and where a number of extinct species are intermingled with forms similar to those of the existing fauna and flora. In Europe the human dwelling-places in caves, rock-shelters and river settlements belong chiefly to the so-called "Reindeer Period," for the most part of glacial or post-glacial age. Metal implements and clay vessels are unknown. Flint, bone, horn and ivory were chiefly used for weapons, implements and ornaments.

The flint implements of the palaeolithic or older Stone Age are distinguished from those of the neolithic by the lack of intelligent handiwork.

They are never pierced or polished, but merely rough-hewn and brought

FIG. 368.

Palaeolithic Flint Implements of successive Ages. *A*, Chellean, 1/2. *B*, Acheulean, 2/3. *C*, Mousterian, 1/1. *D*, Magdalenian, 1/1.

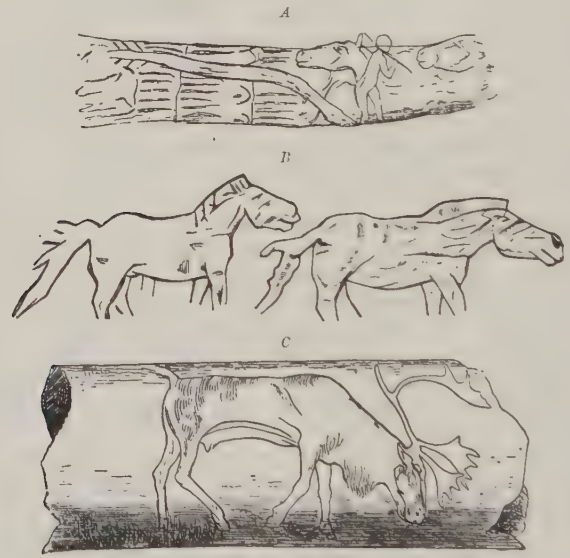


FIG. 369.

Drawings by Palaeolithic Man on bones of Reindeer. *A*, Man with Horses; Dordogne. *B*, Hog-maned Horses; Dordogne. *C*, Reindeer feeding; Kesserloch, near Schaffhausen.

into shape by strokes with another stone, thus being fitted for use as axes, knives, scrapers, lances and arrow-points (Fig. 368). Besides flint, the

bones and antlers of the reindeer were used for fashioning implements and ornamental objects, and of especial interest are the characteristic representations that Man of the older Stone Age carved on bone and ivory (Figs. 369-371). These were evidently done with flint chips, and are not without merit, being easily distinguished as figures of the mammoth, ox, bison, reindeer and horse, possibly also the Saiga antelope. Coloured designs and

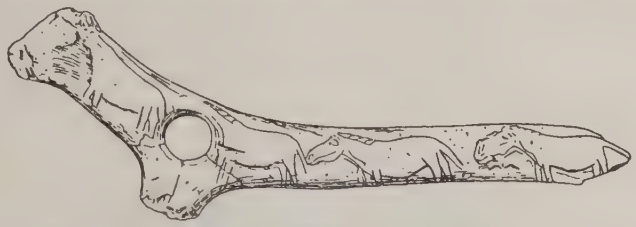


FIG. 370.
Arrow-straightener of reindeer antler, with drawings of Horses. Magdalenian, Dordogne.

incised outlines of these animals were also placed on the walls of caves, the paintings being most abundant in the Dordogne (Fig. 372) and in northern Spain. Carvings and engravings on bone and on slabs of stone are known from the caves in the Dordogne and Belgium, as well as from Schweizersbild and Kesslerloch, near Schaffhausen, drawings of the horse and reindeer being especially noted here. Yet the really artistic products, the carvings on ivory, pertain to a relatively early period, for they certainly occur in an inter-

FIG. 371.
Drawing of Mammoth on ivory. Cave of La Madelaine, Dordogne. 1/3. (After Lartet and Christy.)

glacial deposit, while the Man of Schweizersbild did not live until after the last glaciation, when the Mammoth was very rare and *Rhinoceros antiquitatis* was wholly extinct. However, representations of the Mammoth have been found at Schaffhausen, which are far inferior in accuracy to those from the caves of La Madelaine in the Dordogne. These pictorial delineations not only furnish a convincing argument for the contemporaneity of Man and Mammoth, but the discoveries in Schweizersbild and in the Loess of Bohemia and Moravia equally prove that Man hunted this animal and lived on its flesh, for only thus could the accumulation of its bones here observed be explained. These remains pertain chiefly to young individuals, and are frequently broken open and burnt. Palaeolithic implements are known practically throughout Europe, and are not merely restricted to caves, but also occur in undoubted Pleistocene gravels and clays. The flints

(Fig. 368) were chipped differently at successive periods, and can often be used to determine the age of the deposits in which they are found. The periods are named from the several localities in France in which the characteristic flint implements were first observed, namely, in ascending order, Chellean, Acheulean, Mousterian, Aurignacian, Solutrean, and Magdalenian.

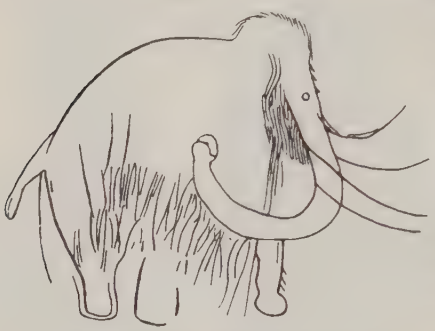


Fig. 372.
Incised outline of Mammoth on wall of Cave of Combarelles, Dordogne. (After Breuil.)

Skeletons and skulls of Man are known in considerable numbers from palaeolithic deposits, though of course many such discoveries have not been accompanied by accurate proof in regard to their age, and really represent bodies buried in prehistoric, neolithic, or even a later time.

The oldest essentially human remains at present known are those already mentioned as belonging to an extinct genus *Eoanthropus*. This Man was undoubtedly a contemporary of *Elephas antiquus* or *E. meridionalis*. A lower jaw from a river deposit at Mauer, near Heidelberg, which may be almost as old, is also essentially human. It is usually referred to *Homo heidelbergensis*, but it is remarkably massive, with a retreating bony chin, and perhaps represents another extinct genus.

The remains of Man are next contemporaneous with *Rhinoceros antiquitatis* and *Elephas primigenius*, and they still differ so essentially from existing Man as to require them to be described as a separate species, *Homo neanderthalensis*, or *H. primigenius*. In comparison with existing Man, all these forms agree in the strong development of the supraorbital ridges, in the slight arching of the skull-cap, in the forward inclination of the occipital surface, in the imperfect development of a bony chin, and in the depth and heaviness of the mandible, as well as in the size of the teeth, and the dental arch (Fig. 373). The femur and tibia are robust; the former being characterised by its curvature, the latter by its retroversion. The first skeleton, of which the skull-cap and a few other parts have been preserved, was found in a cave in the Neanderthal, near Düsseldorf, in 1856. Two other imperfect skeletons were found buried under stalagmite at the mouth of a cave at Spy, near Namur, Belgium, in 1886. Nearly complete skeletons have subsequently been obtained from caves in France; and one from La-Chapelle-aux-Saints (Corrèze), described by Prof. M. Boule,

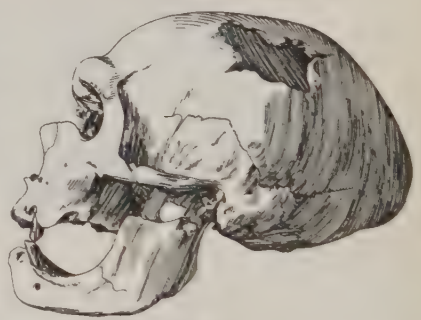


Fig. 373.
Homo neanderthalensis King. Cave of La-Chapelle-aux-Saints (Corrèze). Skull and lower jaw (distorted by loss of teeth during life). 1/4. (After Boule.)

exhibits all its principal features. Fragments, evidently of the same race, found by Kramberger[1] in caves at Krapina, Croatia, differ only in the strong rugosity of the enamel on the teeth.[2] It now appears that Neanderthal Man was not closely related to the Tasmanian blacks, as was once supposed.

Just after Neanderthal Man there lived in Europe races of men which it is difficult to distinguish from those now living. Here belong the skull of Egisheim, Alsace, the skull from the loess, Brünn, and the skull and mandible from Předmost, Moravia, which were certainly contemporaneous with the Mammoth. Still less distinct from existing Man are the skulls, like-

Fig. 374.

Homo rhodesiensis A. S. Woodward. Cave, Broken Hill, Northern Rhodesia. Skull. 1/4. (After A. S. Woodward.)

wise palaeolithic, of Cro-Magnon, Laugerie Basse, and of the Lauter Cave. On the other hand, in the Baoussé Roussé Cave, near Mentone, human relics have been found, which, according to Verneau, possess negroid characters—retreating chin, prognathism, and broad flat nose. They probably belong to the Magdalenian period.

In Africa, the only extinct race of Man hitherto recognised is represented by a skeleton found buried in a cave at the Broken Hill mine, northern Rhodesia.[3] The skull (Fig. 374) has inflated brow-ridges larger than those of Neanderthal Man, and the face is relatively enormous. It is, however, otherwise typically human, and the leg bones resemble those of existing Man. The geological age is uncertain, for *Homo rhodesiensis* occurs with the bones of animals such as still inhabit that part of Africa.

In Australia, one important fossilised skull has been found in the Darling

[1] *Kramberger, Gorjanovic K.*, Der paläolithische Mensch von Krapina in Croatia (Mitteil. Anthropolog. Ges. Wien, 1901, pp. 163-197; 1902, pp. 189-216).

[2] *Schwalbe, G.*, Die Vorgeschichte des Menschen. Braunschweig, 1904.

[3] *Woodward, A. S.*, New Cave Man from Rhodesia, S. Africa. *Nature*, Nov. 17, 1921.—Problem of Rhodesian Fossil Man. Science Progress, vol. xvi., April 1922.—Guide to Fossil Remains of Man in British Museum, ed. 3, 1922.—*Smith, G. Elliot*, Brain of Rhodesian Man, *Nature*, vol. cix., 1922, p. 355.

Downs, Queensland, under circumstances which suggest that it dates back to the period when the giant marsupials, *Diprotodon*, etc., still lived there. It is typically Australoid, but seems to have had the upper and lower canine teeth slightly interlocking.[1]

Pleistocene Man has not been identified with certainty in North America, but there still can be no doubt that Man was associated there with extinct animals. Unquestionable stone implements have been found in Missouri with a *Mastodon* skeleton, in Kansas with remains of extinct species of *Bison*, and at Natchez, Mississippi, lay a human bone near those of *Megalonyx*, *Mylodon* and *Mastodon*. Cope held to the belief that the human relics from North American caves belong altogether to the Recent period, and it is extremely probable that this Man was an immigrant from Asia in company with the Mammoth, and consequently that his arrival in North America happened at a much later time than his first appearance in Europe.

No reliance can be placed on the discoveries in South America. Here also Man was associated with extinct animals, as Lund has observed in the bone caves of Brazil. In the Pampas formation there also occur the marrow-bones and mandibles of deer, *Glyptodon*, *Mastodon* and *Toxodon*, with stone implements and the skull and entire skeleton of Man. The bones and jaws of animals are found broken open and burnt, sometimes also having been fashioned into useful articles. The fresh state of preservation of the Pampas animals, however, renders a relatively great antiquity for these relics extremely improbable, and they may be compared with animal remains from the European neolithic only. In the Eberhardt Cave, on the Gulf of Ultima Esperanza, the extinct *Grypotherium* was apparently kept by Man in a kind of captivity, its skin, hair and excrement still remaining undecomposed. These circumstances permit no doubt to be entertained that the animal in question was contemporaneous with Man, the time of its existence at most probably dating back a few thousand years, and thus coinciding with the historical period of the Old World.

The probability that Man existed in the latest Tertiary—from the Upper Pliocene on—may be considered, for in this period there appear most of the mammalian genera now existing, yet at present discoveries of human relics in undoubted Tertiary deposits are wholly lacking. The flint chips from the freshwater limestone of the Miocene of Thenay, near Pont-Levoy, Loir-et-Cher, and from the Tertiary of Portugal may as little be ascribed to human industry as the flint chips with which the floor of the Libyan Desert is sometimes strewn for miles around. Equally incredible is the notion that the flint chips found by Nötling in the Pliocene of Burma were split off by Man. In Australia, whither Schötensack had sought to transfer the home of Man, supposed human footprints have been discovered in sandstone thought to be of Tertiary age in Victoria, but the exact horizon of this deposit is doubtful. It is still most probable that the genus *Homo* did not originate in Europe, but in Asia.

For the classification and terminology of the Pleistocene and Prehistoric periods, Piette[2] has published the following tabular scheme; other important items, however, have also been inserted here:

[1] *Smith, S. A.*, Fossil Human Skull from Talgai, Queensland. Phil. Trans. Roy. Soc., ser. B., vol. 208, 1918, p. 351.

[2] Centralblatt für Anthropologie, 1901, p. 65.

Subdivision and Characteristics of the Pleistocene and Prehistoric Periods

Climate and Fauna.	Industry.	Characteristics.	Period.
		Transitional period.	Tillousien (Tilloux, Charente).
A. Warm Climate. *Elephas antiquus.* *Rhinoceros merckl.* *Hippopotamus major.*	Large almond-shaped implements, roughly worked on both sides.	Greatest distribution of *Elephas antiquus.*	Chelléen (Chelles, Seine-et-Marne).
		Partial but progressive refrigeration.	Acheuléen (St. Acheul, ? Taubach, Villefranche)
			Krapina ?
B. Cold Climate. *Elephas primigenius.* *Rhinoceros antiquitatis.* *Rangifer tarandus.*	Scrapers and points, one side retouched.	Extensive glaciation.	Moustérien (Le Moustier, Dordogne ; Neanderthal ?).
	Carvings on ivory, various small flints.	Age of sculpture.	Papalien, Éburnéen (Brassempouy, Dordogne ; ? Předmost).
Fauna of the Steppes.		Age of engraving.	Gourdanien, Cervidien (Gourdan, near Montrejeau, Haute-Garonne; Schweizersbild).
C. Cold Damp Climate. Fauna of to-day. *Cervus elaphus.* Migration of people and animals. Entombment of human bones with red colouring matter.	Transitional period. Implements as in the Magdalénien. Flat harpoons of deer horn.	Age of painted rocks.	Asylien. Mas d'Azil. Ariège.
D. Temperate Climate.	Neolithic. Polished implements.	Age of snail and oyster deposits.	Arisien (Arise, near Mas d'Azil).
		Polished axes.	Robenhausien. Earlier pile-dwellings.
Fauna of to-day.	Bronze Age.	Bronze Age.	Morgien. Later pile-dwellings.

OBSERVATIONS ON THE GEOLOGICAL DEVELOPMENT, ORIGIN AND DISTRIBUTION OF MAMMALS.[1]

Up to the present time no mammalian remains have been reported from pre-Triassic deposits. Mammals are even somewhat rare in the Triassic, but are nevertheless represented by two distinctly different types, namely, the *Allotheria* and the *Dromatheriidae*, which remind one of insectivores on the one hand, and polyprotodont marsupials on the other. The *Allotheria* may be divided into the genera *Microlestes* and *Triglyphus* from the Rhaetic Bonebed of Würtemberg, and the genus *Trifylodon* (*Theriodesmus*) from the Karroo strata of South Africa. These forms indicate that the *Allotheria*, which became extinct in the Eocene, were already very widely distributed at this time. The latter type (*Dromatheriidae*) is represented by the small mandibles of the genera *Microconodon* and *Dromatherium* from the Upper Triassic of North Carolina, also possibly by two tiny mandibles which were found a few years ago in the Triassic of Cape Colony and have been described as *Tribolodon* and *Karoomys*. It is very questionable whether these specimens belong to the Mammalia.

The mammalian remains from the Jurassic are decidedly more numerous, for the *Allotheria* as well as the polyprotodont *Marsupialia* during this time develop a considerable variety of forms. In Europe no new forms have lately been discovered from the long known localities of the Great Oolite of Stonesfield, and the "Dirtbed" of Purbeck, England; instead the Atlantosaurus beds of Wyoming and Colorado have yielded a number of mammals, which in part are closely related to well-known forms from England and in part even belong to the same genera as these. The *Allotheria* are represented in England by the genus *Plagiaulax*, and in North America by the genera *Allodon* and *Ctenacodon*. The remaining mammals of the Jurassic have a secodont dentition, and on account of their similarity to the recent genus *Myrmecobius* were classified by Owen with the polyprotodont marsupials. Osborn showed later that several of these forms are very like certain insectivores in dental and mandibular structure, and that the dental formula of one genus, *Peramus*, is absolutely identical with that of the primitive placentals. Other forms,

[1] *Ameghino, F.*, Les Formations sédimentaires de Patagonie. Anal. del Museo de Buenos Aires, vol. xv., 1906.—*Lydekker, R.*, A Geographical History of Mammals. Cambridge, 1896.—*Marsh, O. C.*, Introduction and Succession of Life in America. Amer. Assoc. for Advancement of Sci., Nashville, 1877. *Matthew, W. D.*, Classification of the Freshwater Tertiary of the West. Bull. Amer. Mus. Nat. Hist., New York, 1899.—Cenozoic Mammal Horizons of Western North America. Bull. U.S. Geolog. Survey, No. 361, 1909.—*Osborn, H. F.*, The Rise of the Mammalia in North America. Amer. Assoc. for Advancement of Sci., Madison, 1893. Correlations between Tertiary Mammal Horizons of Europe and America. Ann. N.Y. Acad. Sci., vol. xiii., 1900.—*Stehlin, H. G.*, Die Säugetiere des schweizerischen Eocans. Abh. Schweiz. Paläont. Ges. 1903 1910.—Mammifères cocènes et oligocènes du bassin de Paris. Bull. Soc. Géol. de France, 1909.

however,—the *Triconodontidae*—indicate by the shape of the angle of the lower jaw that they doubtlessly belong to the *Marsupialia*. Because of the incompleteness of existing specimens it is well not to go further in dividing the remaining secodont forms into families and orders, but rather to ascribe them to the marsupials in general.

Mammalian remains from the **Cretaceous** were first discovered in 1882. The first finds from the Wealden strata in England consisted of small teeth of the genus *Plagiaulax*, already known from the Jurassic. Soon after Cope discovered a tooth of *Meniscoëssus* in the Laramie strata of Dakota, and a little later Hatcher collected numerous teeth, mostly isolated, in Wyoming and Colorado. Marsh founded many new genera and species on these specimens. These have, however, been considerably revised by Osborn. Since the majority of the teeth belong to the *Allotheria*—*Ptilodus*, *Meniscoëssus*—our knowledge of fossil mammals has not been greatly increased by these discoveries, but they are of considerable interest because they bridge the gap between the Jurassic and Tertiary forms of this group. Osborn even believes that a few of the rather infrequent tritubercular and tuberculo-sectorial forms can be determined as Creodonts (*Pediomys*), and that others (*Protolambda*) can be considered ancestors of *Pantolambda*, also of the *Amblypoda*. If there were more and better preserved specimens far better phylogenetic conclusions could be drawn.

Eocene.

The beginning of the Tertiary marks a significant turning-point in the development of mammals. At this time several orders which indisputably belong to the Placentals have their origin, whereas the *Allotheria* gradually become extinct. The oldest mammalian remains from the Tertiary of Europe were discovered in the neighbourhood of Rheims. Lemoine distinguishes in this region two chronologically superimposed faunas, that of Cernays and that of Agéia. The former contains representatives of *Allotheria*—*Neoplagiaulax*,—of *Creodontia*—*Arctocyon*, *Dissacus*, *Hyaenodictis*,—of certain questionable insectivores—*Plesiadapis*, *Protoadapis*, *Adapisorex*,—of *Condylarthra*—*Pleuraspidotherium*—and of *Orthaspidotherium*, which seems to be the ancestor of *Anoplotherium*. The fauna of Agéia will be discussed more fully later. Of course these two faunas demand urgent reconsideration because of the very strange illustrations furnished by Lemoine. The specimens of the approximately contemporary fauna of the Cernaysian of the Puerco beds of New Mexico and of the somewhat more recent Torrejon beds of New Mexico and Montana are more abundant. The former locality still contains several *Allotheria*, among which are the important genera *Neoplagiaulax* and *Polymastodon*, several *Creodontia*—*Triisodon*, *Oxyclaenidae*,—several *Condylarthra*—*Mioclaenus*, *Oxyacodon*, *Protogonodon*, *Periptychidae* and *Taeniodontia* (*Ganodonta*). In the latter locality are the last of the *Allotheria*, and the *Creodontia* become more varied. They are represented by the *Arctocyonidae*, *Mesonychidae*, *Oxyclaenidae*, *Triisodontidae* and the *Miacidae*, already closely affiliated with the true carnivores. The *Condylarthra* are represented by many *Mioclaenidae*, by the earliest *Phenacodontidae* and *Periptychidae*, the *Taeniodontae* (*Ganodonta*) by *Conoryctes* and the insectivores by the *Mixodectidae*. Simultaneous with these appeared the first amblypod, *Pantolambda*.

The difficulties connected with a systematic discussion of this period can be scarcely overcome, for the structure of many of these forms is very primitive, the dentition is almost always composed of incisors, canines and premolars which are very similar to those of carnivores, the molars are bunodont or secodont—the lower ones more or less tuberculo-sectorial and the upper ones tritubercular,—the bones of manus and pes are almost always of very indefinite shape, the humerus has an entepicondylar foramen and the femur often has a third trochanter, and the powerful fibula does not meet the calcaneum. Manus and pes have five digits and are, as far as known, somewhat plantigrade. The end-phalanges are developed neither as a real hoof nor as a real claw. It is therefore hardly to be wondered at that so many species have several times changed their position not only within the genus but also within the order, and that even the divisions between families and orders have often been shifted.

These facts furnish a weighty argument for the truth of the theory of evolution, since the uniform structure of the earliest placentals permits no other conclusion than that all or at least most of the orders of higher mammals may be traced back to one or the other of very few primitive forms. The fauna of Rheims and of the Puerco and Torrejon beds is usually designated at the present time as **Basal Eocene.**

The **Lower Eocene** comprises in Europe the Sparnacian and Yprèsian London Clay, the Teredina sands of Epernay, the Landénian of Erquelinnes and Orsmael in Belgium, and the Plastic Clay and Lignite of the Paris Basin; in North America the Wasatch beds of Wyoming and New Mexico and the somewhat more recent Wind River beds of Wyoming and Colorado. In Europe the affiliations with the older fauna of the Cernaysian still seem to be close, at any rate the Agéian and Landénian still contain *Plesiadapis*, *Protoadapis*, *Dissacus* and *Didymictis*. Notwithstanding, true rodents—*Plesiarctomys*,—well-developed *Creodontia*—*Protoproviverra*, *Palaeonictis*, *Pachyaena*,—true perissodactyls—*Hyracotherium*, *Propachynolophus*, *Pachynolophus*, *Chasmotherium* and *Lophiodon*,—an artiodactyl—*Protodichobune*,—and according to some also a condylarthran—*Phenacodus* ?—as well as an amblypod genus *Coryphodon*, which reaches the zenith of its development in the Wasatch and Wind River beds, all already appeared at this time. Whereas in Europe only the artiodactyls and perissodactyls, the rodents and certain creodonts present a new link in the history of mammals, in North America the gap between the fauna of the Basal and Lower Eocene seems of somewhat greater significance. Real primates—*Anaptomorphidae*, *Pelycodus*, *Notharctus*,—numerous insectivores which are very closely related to the primates—*Mixodectidae*,—and the *Hyopsodontidae*, rich in genera and partly deviating from the true insectivores on account of size—*Esthonyx*, *Palaeosinopa*,—partly very similar to them—*Palaeictops*,—also the earlier rodents—*Paramys*,—and almost all the families of the later *Creodontia*—*Palaeonictidae*, *Oxyaenidae*, *Hyaenodontidae* and *Mesonychidae*; all these forms appear in the North American fauna of this period. The *Miacidae* also develop a considerable variety of forms. Those that appear for the first time are the *Meniscotheriidae*, also many perissodactyls—*Heptodon*, *Systemodon*, *Eohippus* and *Lambdotherium*,—and certain artiodactyls—*Trigonolestes*, *Parahyus*. On the other hand the *Ganodonta*—*Calamodon*, *Stylinodon*,—*Coryphodon* of the amblypods, and the *Phenacodontidae* of the *Condylarthra* are all quite closely allied to forms of the Torrejon. The difference between the

earlier *Mesonychidae*, *Arctocyonidae* and *Miacidae*, and their Lower Eocene representatives, is not so great that a genetic connection between these faunas must be absolutely denied.

Though the fauna of the Lower Eocene in North America has yielded a large number of species, genera and families, it is only during the **Middle Eocene** that a varied animal distribution appears in Europe. The most important localities in Europe are Argenton (Indre), the Parisian Calcaire Grossier, La Livinière, Cesseras and Issel in southern France, Bracklesham in England, Buchsweiler in Alsace and the Bohnerz of Lissieu, Chamblon and Egerkingen. The fauna of the Bohnerz was widely considered up to a short time ago to be merely a mixture of mammalian teeth from many different strata of the Tertiary, since the greatest variety of animal remains seemed to have been found in the same locality. This was so, largely because experts only supervised the excavations in exceptional cases, and because the remains were segregated according to the state of preservation and the place of their origin in the different strata. Closer observation, however, made possible a very exact division between the different faunas of the south German and the Swiss Bohnerz. Therefore we can well state that only contemporaneous remains were interned in a single stratum.

In the fauna of the European Middle Eocene the perissodactyls are without a doubt the most important fossils. Those resembling the tapir are represented by *Chasmotherium* and *Lophiodon*, those most like horses, by *Palaeotherium*, *Propalaeotherium*, *Paloplotherium*, *Lophiotherium*, *Anchilophus* and *Pachynolophus*. The artiodactyls, on the contrary, are very sparsely represented in the earlier part of this period, in the lower Lutetian only by the *Dichobunidae,—Dichobune*, *Meniscodon*, and *Anoplotheriidae,*—by *Catodontherium*, *Dacrytherium* and by the somewhat puzzling genus *Tapirulus*. Only in the Upper Lutetian are found the *Suidae—Cebochoerus* and *Choeromorus,*—the *Anthracotheriidae—Haplobunodon*, *Lophiobunodon*, *Rhagatherium,*—the *Anoplotheriidae—Mixtotherium* and the small *Leptotheridium,*— and the first *Xiphodontidae—Pseudamphimeryx*, *Dichodon* and *Haplomeryx*. Rodents, *Creodontia*, and primates are by no means lacking, but they are principally restricted to the Swiss Bohnerz. The American representatives of this order have been more exactly studied. The primates found in the Bridger beds are represented by the *Notharctidae* and the *Anaptomorphidae*, the insectivores by the *Pantolestidae*, *Hyopsodontidae*, *Mixodectidae*, and by the giant *Tillotheridae—Tillotherium*—as well as by several small forms closely allied to the *Talpidae*, *Centetidae* and *Leptictidae*. The *Miacidae* develop the greatest variety of species among carnivores—*Viverravus*, *Miacis*, *Vulpavus*. The *Oxyaenidae—Patriofelis*, *Limnocyon*, *Thinocyon*—are likewise well represented, and the *Mesonychidae* during this period attain a specialization of the extremities similar to that of present-day dogs. The primitive *Hyaenodontidae—Sinopa* —are somewhat richer in forms here than in the Wasatch beds. The same is also true of rodents, *Paramys* and *Sciuravus*, to which several new genera are added about this time. In North America, as is the case in Europe, the perissodactyls become richer in forms in the Lower Eocene; the number of species of the *Tapiridae,—Helaletes*, *Isectolophus*—and of the *Equidae* —*Orohippus*—remains approximately the same, but the *Titanotheriidae*— —*Palaeosyops*, *Limnohyops*, *Telmatherium*—become more varied in form. The artiodactyls are represented only by *Dichobunidae*, which, however, manifest a greater wealth of forms—*Homacodon*, *Sarcolemur*, *Helohyus*—than in the

Wasatch beds. The *Condylarthra* have become entirely extinct and the *Amblypoda* attain their zenith in the tremendously overpowering *Dinoceratidae*. The *Taeniodontae* (*Ganodonta*) are only represented by a single genus, *Stylinodon*, which is distinguished, however, as a very advanced type compared to the earlier forms, on account of its hypsodont teeth. Special mention is due to the nearly toothless genus *Metachiromys*, which Osborn claims is an armourless relative of the armadillo.

The wealth of mammalian forms in Europe in the Upper Eocene—Bartonian and Luidian—increases. The number of forms in North America—Upper Bridger beds of Wyoming and Uinta beds of Utah—on the contrary, diminishes most noticeably. The Bartonian is developed in southern France, Minervois, Robiac and Castres, as "Sables moyens" in the Parisian basin and as sands of Headonhill and Bracklesham in England. The Bohnerz fauna of Mauremont and even a certain portion of the Phosphorites of Quercy also belong to this period. The Luidian faunas originate from the Paris Gypsum, from the Lignites of Débruge (Vaucluse), from the Marls of St. Hippolyte de Caton (Gard), from Lamandine (Tarn et Garonne) and from the Bembridge Marls of England. The Bohnerz of Mauremont and Obergösgen and the Phosphorites of Quercy contain numerous species characteristic of the Luidian fauna. The fauna of the European Upper Eocene taken as a whole varies only slightly from that of the Middle Eocene. The perissodactyls are also the predominating element during this period. *Lophiodon* has, however, reached the height of its development in the Bartonian, and *Chasmotherium* also appears for the last time—as do also *Propalaeotherium* and *Pachynolophus*. On the other hand, the genera *Palaeotherium*, *Paloplotherium*, *Lophiotherium* and *Anchilophus*, the two latter with few species, flourish. The artiodactyls gradually become more numerous. Of the *Suidae*, *Choeropotamus* now appears in addition to *Cebochoerus*, which already existed at an earlier period. The *Anthracotheriidae*, already represented,—*Haplobunodon*, *Rhagatherium*—continue in their development. The same is true of the *Anoplotheriidae*,—*Mixtotherium*, *Catodontherium*, *Dacrytherium* and *Leptotheridium*, now associated with *Anoplotherium* and *Diplobune*,—and of the *Xiphodontidae*,—*Dichodon*, *Pseudamphimeryx*, *Haplomeryx*, *Xiphodon* and *Amphimeryx*. The *Dichobunidae*—also *Tapirulus*—do not develop further, but a new family, the *Caenotheriidae*, represented by the genus *Oxacron*, appears for the first time. The carnivores, of which only the *Hyaenodontidae*—*Sinopa*, *Proviverra* and *Propterodon*,—the *Miacidae* and the *Amphicyonidae* exist in the Middle Eocene of Europe, show a much greater variety, for the *Hyaenodontidae* become subdivided into several new genera—*Hyaenodon*, *Pterodon*, *Quercytherium*, *Cynohyaenodon*. The *Miacidae* are represented by the complete remains of "*Viverra*" (*Viverravus*). A small Oxyaenid—*Thereutherium*—and numerous species of the genus *Cynodictis*, the most primitive canine with viverra-like skeleton, appear. Of the rodents, the *Sciuroides* and *Plesiarctomys* apparently originate—probably also *Theridomyinae* and *Cricetodon*—in the Lutetian and become somewhat richer in species in the Upper Eocene. The same may be said also of the primates—*Adapis*, *Cryptopithecus*, *Microchoerus* and *Necrolemur*. In the Luidian there are real *Didelphyidae* already, and in the Lutetian apparently *Insectivora* and *Chiroptera* resembling *Talpa*. In North America the fauna of the Upper Eocene presents a marked contrast to that of Bridger because of the scarcity of forms. The lower strata of the Upper Eocene contain another primate—*Notharctus*,—a few

Oxyaenidae, *Mesonychidae*, *Paramys* of the rodents, *Hyrachyus*, *Amynodon*, *Heptodon*, *Dolichorhinus* and *Telmatherium* of the perissodactyls, *Achaenodon* of the artiodactyls and *Leptotragulus* of the earliest *Camelidae*. Particularly characteristic of this fauna is the presence of the last dinoceratid, *Eobasileus*. In the somewhat more recent Uinta fauna we find the last *Miacidae*, *Oxyaenidae*, *Mesonychidae*, the first *Canidae*, *Procynodictis*, and the last of the *Hyopsodontidae*. A new rodent type, possibly one of the *Geomyidae*—*Protoptychus*—appears to take the place of *Paramys*, a genus which is gradually disappearing. The perissodactyls have a somewhat greater variety of forms than in the foregoing fauna, for with the forms of *Amynodontinae* and *Palaeosyopinae*—*Diplacodon*, *Telmatherium*, *Manteoceras*—which appeared at an earlier time, are associated a tapir, *Isectolophus*, and the *Epihippus*, the genus of *Equidae* which is so extraordinarily important in the developmental history of the horse. The hyracodontid—*Hyrachyus*—however is substituted by the more slimly built form, *Triplopus*. The artiodactyls also undergo a considerable increase in forms. Instead of the extinct genus *Achaenodon* the first *Agriochoeridae*—*Protoreodon* and *Protagriochoerus*—appear and the *Camelidae* become more numerous—*Leptotragulus*, *Protylopus*, *Camelomeryx*. The genus *Bunomeryx*, which probably is the forerunner of *Protoceras*, also appears.

The careful study of these faunas of the northern hemisphere has in no way confirmed the supposition that a considerable exchange of forms took place between North America and Europe during the whole Eocene, for the number of forms common to both continents is increasingly small. But these researches have shown that there are a large number of co-ordinate forms which follow the same or a very similar progressive development on both continents, and that the presentation of a number of unusually complete genetic sequences is possible. As a rule, however, no gradually increased branching from a single type form is found, as might be supposed, but many species in one genus arise simultaneously, and these then form parallel lines of development. The careful researches upon the European perissodactyls and artiodactyls, for which we are indebted to Stehlin, present many such genetic lines of development, which extend sometimes from the Lower Eocene up to the Oligocene. The generic lines of development are indicated here only in the genera *Choeropotamus*, *Cebochoerus*, *Choeromorus*, *Rhagatherium*, *Diplobune*, *Pseudamphimeryx*, *Dichodon*, *Anchilophus*, *Palaeotherium*, *Paloplotherium* and *Lophiodon*. The study of the creodonts, the rodents and the primates will aid us soon to complete this series. Osborn, Wortman and Matthew have succeeded in completing similar lines of development from material found in North America. These studies have been made to include not only the perissodactyls and artiodactyls but also the primates, the creodonts, the rodents, the *Ganodonta* and the *Amblypoda*. In contemplating these parallel lines of development it is particularly surprising to find in Europe at least the origin of a new genus from geologically older genera exceptional. This can scarcely be explained otherwise than by repeated immigration from a centre of development as yet unknown but which is sought at times in Asia, in an Arctic continent, and in the north-eastern part of North America. This is a problem which can only be solved by future discoveries. The advances made along these parallel lines of development are apparent above all in the great increase in bulk, among the perissodactyls and sometimes among the artiodactyls, in the complicated structure of the premolars, in the specialisation of

certain incisors and of the canines, and among the ganodonts in the development of hypsodont, rootless teeth. The creodonts, however, which originally have tritubercular, *i.e.* tuberculo-sectorial, molars, usually specialise so that on the uppers a long cutting metastyle arises and the protocone becomes reduced, and on the lowers the metaconid often disappears and the talonid becomes noticeably reduced; the protoconid and paraconid may also become converted into a long cutting surface. At times the number of molars becomes reduced, and in the case of the parent forms of the true carnivores a certain reduction in the rear molars occurs. As regards the extremities, they are only known in a few cases among European mammals, but the specimens which have been found show that the reduction of the lateral digits took place early in the developmental history not only of the artiodactyls but also of the perissodactyls. The third and fourth digits assumed the principal function in the case of the former, but only the third in the case of the latter, though not infrequently the manus retains four and the pes three digits. Even the creodonts sometimes lose the first digit.

The marine mammals also appear for the first time in the Eocene. The whales are only represented by the family *Zeuglodontidae*, but they are rather widely distributed already in the southern part of North America, in Europe, Egypt and on the island of New Zealand. The *Sirenia* are found in the West Indies, Europe and Egypt. The former very probably may be traced back to the creodonts, the latter are derived from the same form as the *Proboscidea*. Both doubtless developed from terrestrial placentals.

Oligocene.

The Oligocene in North America exhibits a much sharper division into successive faunas, and at the same time a considerably greater richness in forms than in Europe. The White River beds of Nebraska, Dakota, Montana, Colorado and Wyoming are readily divisible into three horizons. The lowest, as well as the *Titanotherium* bed, which occurs in the Cypress Hills, Canada, is characterised by the gigantic *Titanotheriidae*, a family of perissodactyls, and by insectivores resembling the *Chrysochloridae*; the middle, by the abundance of the *Agriochoeridae* and the richness in insectivores and *Didelphyidae*; the uppermost, by the genera *Leptauchenia* and *Protoceras*. In the latter horizon, on the other hand, the *Hyaenodontidae*, which, with *Elotherium*, *Anthracotherium*, *Ancodus*, and the pig *Perchoerus*, represent a European faunal element, and the *Leptictidae* among insectivores are already completely extinct. Common to all divisions of the White River Oligocene are *Canidae—Amphicyoninae* and *Cynodictinae*, *Mustelidae*, primitive *Felidae—Dinictis*, *Hoplophoneus*, numerous rodents—especially *Castoridae*, *Ischyromyinae*, and *Leporidae*, among perissodactyls the forerunners of the horses—*Mesohippus*, tapirs, and rhinoceroses. Nevertheless, of the tapirs *Colodon*, and of the rhinoceroses *Hyracodon* and *Metamynodon*, are restricted to the older horizons, while *Protapirus* first appears somewhat later, and *Aceratherium* on the contrary ranges throughout the Oligocene. In addition to the *Camelidae* and *Agriochoeridae*, which pass upwards from the Uinta beds and now exhibit striking advances in their organisation in the genera *Poebrotherium*, *Agriochoerus*, *Oreodon*, and *Leptauchenia*, there are here among selenodonts the small *Hypertragulidae* and, finally, *Protoceras*;

among bunoselenodonts *Anthracotherium* and *Ancodus*; and among bunodonts *Elotherium*, the *Leptochoeridae* and a true pig—*Perchoerus*.

In Europe the Oligocene is characterised by the preponderating occurrence of the genus *Anthracotherium* and the presence of numerous primitive *Acerotherium*-like rhinoceroses. A rather rich fauna restricted to a short period of time is known from Ronzon, Haute Loire. The genus *Anthracotherium* is indeed missing in this locality, but it certainly lived at the same time as *Ancodus*, which is so characteristic of Ronzon, as proved by the discovery of the two together at Hampstead, in the Isle of Wight. Contemporaneous with the marls of Ronzon are the Bohnerz of Vehringen and Ulm, the limestone of Brie, the sands of Fontainebleau, a large part of the phosphorite of Quercy, the lignite of Dalmatia and Northern Italy—Monte Bolca, Monteviale, and of Bohemia, and the asphalt deposits of Lobsann in Alsace. The locality of Calaf, near Barcelona, is of special interest, because here *Diplobune* also occurs in association with *Ancodus*. Besides *Diplobune* there also range upwards from the Eocene into the Oligocene *Paloplotherium* and presumably *Palaeotherium*; among smaller artiodactyls, *Amphimeryx*, *Caenotherium*, and *Plesiomeryx*, with *Metriotherium*, *Dichobune*, and *Tapirulus*; among carnivores, *Hyaenodon*, *Amphicyoninae*, and *Cynodontinae*—the supposed forerunners of the bears; among rodents, *Theridomys*, *Sciuroides*, and *Pseudosciurus*; among insectivores, *Erinaceinae*; and marsupials. Hence, if these forms are regarded as of prime importance, it may be said that we are dealing merely with an impoverished Eocene fauna. Nevertheless, while these earlier elements, such as the Eocene types of perissodactyl, are gradually becoming extinct, there is no inconsiderable development of new forms; there appear rhinoceroses — among them *Cadurcotherium* — *Protapirus*, *Chalicotherium*, forerunners of the deer—*Gelocus*, *Bachitherium*, *Prodremotherium*—and of the pigs —*Palaeochoerus*, *Doliochoerus*—also the genera *Anthracotherium*, *Ancodus*, and *Elotherium*; and among carnivores, a small *Hyaenodon*, numerous mustelines—*Palaeoprionodon*, *Stenogale*, *Stenoplesictis*, *Plesictis*—besides forerunners of bears—*Cynodon*, *Pachycynodon* and *Cephalogale*. There also belong first to the Lower Oligocene the numerous insectivores, bats, and the greater part of the rodents from the Phosphorites, chiefly *Theridomys*, but also *Protechimys*, *Nesokerodon*, *Cricetodon*, and *Eomys*.

The next younger fauna—Stampian—from the marls of Cournon, Peublanc, and Gergovia, in the Auvergne, St. Henri near Marseilles, and Briatexte (Tarn), forms indeed the continuation of the fauna of Ronzon, as shown by the presence of the last *Hyaenodon* and the higher stage of development of the rodents—*Archaeomys*, *Issiodoromys*,—but it is incomparably poorer in species. The most important forms are a large *Anthracotherium* with nearly unreduced side toes, *Lophiomeryx*—which also occurs in the *Cyrena*-marls of the Mainz Basin—besides *Dremotherium* and *Amphitragulus* and the first *Ochotonidae*—*Titanomys*. With these there still occur *Caenotherium* and *Plesiomeryx*, as well as *Palaeochoerus*, *Rhinoceridae* and *Tapiridae*.

The youngest Oligocene fauna is that of La Milloque, Gannat, to which the mammalian remains from the lignites of Cadibona, Rochette and Rott belong. It has yielded only few species, among which, however, the true *Anthracotherium magnum* and the small *Microbunodon* are of special importance on account of their abundance. A large part of the European Oligocene, moreover, is of marine origin, and is then characterised by numerous remains

of sirenians—*Halitherium*—while cetaceans are very rare, and represented only by *Squalodontidae*, mingled with which occur isolated remains of land mammals —*Apterodon*, *Anthracotherium* and primitive rhinoceroses.

Miocene.

In North America the Miocene begins with the John Day beds of Oregon, which are characterised especially by the abundance of rodents and by the presence of *Diceratherium* and *Promerycochoerus*. From the White River Oligocene there pass upwards the perissodactyls *Aceratherium*, *Protapirus* and *Mesohippus*, and the artiodactyls *Elotherium*, *Perchoerus*, *Agriochoerus*, *Paratylopus* and *Hypertragulus*; but with the former are newly associated the first *Diceratherium*, *Miohippus*, and the chalicothere *Moropus*, with the latter, *Eporeodon* and *Promerycochoerus*. The numerous carnivores are distributed among the genera *Nothocyon*, *Mesocyon*, *Temnocyon*, *Enhydrocyon*, *Nimravus*, *Pogonodon*, and *Hoplophoneus*; the rodents, among the genera *Prosciurus*, *Steneofiber*, *Entoptychus*, *Pleurolicus*, *Meniscomys*, *Mylagaulodon*, *Paciculus*, *Peromyscus*, and *Lepus*. The somewhat younger faunas of the Harrison beds of Montana, the Rosebud beds of South Dakota, the Monroe Creek beds of Nebraska, etc., are on the whole rather poor in species and genera. As characteristic and at the same time new types there are of interest the carnivore genera *Phlaocyon*, *Cynodesmus*, *Oligobunis*, *Megalictis* and *Aelurocyon*, the perissodactyls *Parahippus*, *Anchitherium* and *Miohippus*, and the artiodactyls *Dinohyus*, *Desmathyus*, *Mesoreodon*, *Merycochoerus*, *Merychyus*, *Leptauchenia*, *Stenomylus*, *Protomeryx*, *Oxydactylus*, and especially the genus *Blastomeryx*, a Hypertragulid. The immediately succeeding faunas of the Deep River and Flint Creek in Montana, of Pawnee Creek in Colorado, and the Mascall beds in Oregon, exhibit no such diversity as that of the North American Oligocene. They comprise essentially only the successors of the earlier *Canidae*, *Rhinoceridae*, *Equidae*, *Agriochoeridae*, *Camelidae* and *Suidae*, but they have almost all so much changed that the recognition of many new genera seems necessary. Of *Canidae* may be mentioned *Tephrocyon*, *Cynarctus*, *Amphicyon* and *Canis*; of *Felidae*, *Pseudaelurus*; of *Rhinoceridae*, *Caenopus*, *Aphelops* and *Teleoceras*; of *Equidae*, *Merychippus*, *Hypohippus* and *Parahippus*; of *Suidae* a dicotyline, *Hesperhyus*; of *Agriochoeridae*, *Merycochoerus*, *Promerycochoerus*, *Mesoreodon*, *Merychyus* and *Cyclopidius*; and of *Camelidae*, *Miolabis*, *Procamelus*, *Protolabis* and *Alticamelus*. The rodents are represented almost entirely by *Mylagaulus*-like forms. The first appearance of *Proboscidea* — *Tetrabelodon* (*Trilophodon*)—in North America, however, gives to these younger faunas special importance. They also appear strange from the occurrence of the rhinoceroses *Aphelops* and *Teleoceras*, of *Palaeomerycinae*, and of the *Mustelidae*, *Potamotherium* and *Mustela*, which are reminiscent of European conditions. *Blastomeryx* and *Merycodus* on the other hand are certainly autochthonous.

While the composition of the fauna just described certainly indicates an immigration of Old World elements, the next younger fauna is evidently the product of the quiet further development of the types already present without any foreign intrusion. Unfortunately, it is far behind the older North American faunas in variety, but this is partly compensated for by a remarkable abundance of individuals. The somewhat older Arikaree stage has apparently a wider distribution—Nebraska (Niobrara), South Dakota, Montana, New Mexico and Texas—than the younger Olagalla stage in Kansas and Nebraska,

which is certainly represented also by scattered remains in Florida and Oregon. In time both stages come between the European Upper Miocene and Lower Pliocene, for generally a strict correlation of the North American and European faunas appears scarcely justifiable, and we are rather dealing with an alternation in time. The *Canidae* are represented by *Aelurodon*, *Amphicyon*, *Dinocyon*, *Canis*, *Ischyrocyon*; the *Mustelidae* by *Mustela*, *Putorius* and *Potamotherium*, *Lutra* and *Brachypsalis*; the *Felidae* by *Machairodus* and *Pseudaelurus*; the *Proboscidea* by several well-characterised species of *Tetrabelodon* (*Trilophodon*); the *Rhinoceridae* by the last but very abundant species of *Teleoceras*, *Peraceras* and *Aphelops*. The number of the described species of the *Equidae*, *Protohippus* and *Neohipparion*, from these deposits is very large, but with these there have also been preserved more primitive forms, *Hypohippus*, *Parahippus* and *Merychippus*. Among artiodactyls occur *Suidae*—*Platygonus*, *Prosthenops*—and *Camelidae*—*Procamelus*, *Protolabis* and *Pliauchenia*. The *Agriochoeridae* gradually become extinct with the genera *Promerycochoerus* and *Merychyus*, while *Palaeomeryx*-like deer, such as *Blastomeryx* and the antilocaprid *Merycodus*, become rather numerous. Finally, the rodents are represented by the genera *Sciurus*, *Palaearctomys*, *Dipoides*, *Sigmogomphius*, *Mylagaulus*, *Epigaulus*, *Geomys*, *Hesperomys*, *Panolax* and *Lepus*.

As the lower limits of the European Miocene may best be taken the freshwater deposits of Ulm and Mainz, which are characterised by the presence of *Helix rugulosa*. Of the same age also are the freshwater limestone of St. Gérand-le-Puy, the asphalts of Pyrimont-Challonges, Savoy, and the lignites of Brüx. Of Oligocene types there still occur here especially numerous *Caenotherium* and *Palaeochoerus*, besides the carnivores, *Palaeogale*, *Plesictis*, *Stenogale*, *Amphictis* and *Cephalogale*; also the last marsupials. The perissodactyls—*Chalicotherium*, *Paratapirus*, *Aceratherium* and *Diceratherium*—are only advanced developmental stages of previous types. The same remark applies to the *Cervicornia*, *Amphitragulus* and *Dremotherium*. Among the carnivores, *Amphicyon*, *Potamotherium* and *Herpestes* are conspicuous; among rodents, *Steneofiber*, *Plesiospermophilus*, *Myoxus*, *Cricetodon* and *Titanomys*. Their derivation from types previously represented in Europe seems in some respects doubtful, at least for part of these genera. The insectivores and bats are closely related to living forms, and belong in part even to existing genera. The *Anthracotheriidae* are now represented by a new type, *Brachyodus*.

After this period the sea again took possession of a great part of the middle of the European continent, so that remains of land mammals in the **Middle Miocene** are somewhat rare, and are only preserved in greater number in places which were not submerged, such as near Tuchorschitz in Bohemia and on the Jurassic plateau of Solenhofen, Bavaria. They belong to a fauna which agrees essentially with that of the Upper Miocene, but has still in common with that of the Lower Miocene the genera *Brachyodus*, *Palaeochoerus*, *Amphicyon*, *Cephalogale*, and *Plesictis*. The *Caenotheriidae* are almost, the marsupials completely, extinct. Of the deer—*Palaeomeryx*—the smaller are already characterised by the possession of antlers; the rhinoceroses—*Aceratherium*, *Diceratherium*—are evidently in part the direct successors of previous types, but a new form, *Brachypotherium*, occurs with them. The most important event, however, is the first appearance of the *Proboscidea* in Europe of the genus *Tetrabelodon*. In the sands near Orleans there also occurs *Dinotherium*, besides *Anchitherium*, and even already an anthropoid ape, *Pliopithecus*. The marine Miocene, unlike the Oligocene, contains not only *Sirenia*—*Halitherium* still with *Metaxytherium*—

and *Squalodontidae*, but also numerous modern toothed whales, among which are *Physodon*, *Acrodelphis*, *Cyrtodelphis* and *Delphinus*, besides even a whalebone whale, *Plesiocetus*. Seals also—*Phoca*—now appear.

While the faunas of the Eocene and Oligocene, and even of the Lower Miocene, are on the whole restricted to very few localities, the fauna of the **Upper Miocene** is spread over almost the whole of middle Europe, and is found also near Lisbon and Madrid and in southern Russia. It will suffice to mention, among the numerous localities, only Sansan (Gers), La Grive St. Alban (Isère), Steinheim, Georgensgmünd, Oeningen, the Bavarian-Swabian upland, the lignites of Steiermark, and the land-snail limestone of Oppeln in Silesia. From the Lower Miocene there survive almost unchanged the *Amphicyoninae*, *Viverridae* and *Mustelidae*; but there also appear now forerunners of *Meles*—*Trochictis*—true bears—*Ursavus*—and especially numerous *Felidae*, *Machairodus*, as well as true *Felis*. The rodents, bats and insectivores are essentially the successors of the genera occurring in the Lower Miocene, and the only new genus is *Galerix*, which is represented almost everywhere. Among the artiodactyls, although they are very numerous, there are only small accessions, such as primitive antelopes with a deer-like dentition, and *Hyaemoschus*, which in some ways replaces the extinct *Caenotheriidae* and *Brachyodus*. On the other hand, numerous species of *Palaeomeryx* of different sizes, among which the small and medium-sized forms are now also provided with antlers, seem to be only further developments of the various Lower Miocene species of *Amphitragulus*. Among *Suidae* also there is a direct genetic connection with earlier forms, for *Hyotherium* and the genus *Sus*, which appears here for the first time, are the descendants of *Palaeochoerus*, while *Listriodon* is descended from *Doliochoerus*. Among the perissodactyls, *Chalicotherium*, the tapirs, and *Aceratherium* are easily derivable from Lower Miocene forms; and *Brachypotherium* and *Ceratorhinus* have at least forerunners in the Middle Miocene, where also, as we have seen, *Anchitherium* is recognisable for the first time. In the Middle Miocene there must also have been a slight immigration from a hitherto unknown region, which, however, was likewise in connection with North America. To this region Europe owes the immigration of the perissodactyls already mentioned, besides the *Felidae* and the genus *Galerix*. On the other hand, the *Proboscidea*, *Tetrabelodon* and *Dinotherium*, arriving at the same time, as well as the apes, *Pliopithecus*, can only have come from Africa.

Pliocene.

If the Upper Miocene mammal fauna has a wide distribution in Europe, this is still further the case with that of the **Lower Pliocene** or Pontian stage. In south Germany, indeed, except at Eppelsheim, near Worms, and in certain Bohnerzen of the Swabian Alps, no remains of mammals have been left; in France also, such are known only from Cucuron and Mont Léberon (Vaucluse) and from the neighbourhood of Lyons; but it is probably very widely spread over the Spanish peninsula—it is known from the region of Lisbon as well as from Concud, in the province of Teruel—while in Eastern Europe remains of this fauna are found from the Vienna basin as far as south Russia, and even in Roumania. It is especially well developed in Greece, at Pikermi in Attica; in the western end of Asia Minor—the island of Samos; and in western Persia, at Maragha; but the farther east the localities, the

more numerous are the elements foreign to the European fauna, especially among the ruminants. While in Europe the antelopes play a comparatively small part, and the deer consequently are better represented, the latter disappear almost completely in the east, and the antelopes assume a correspondingly rich development. In Central Europe the Lower Pliocene fauna, apart from the presence of *Hipparion* instead of the extinct genus *Anchitherium*, is only a continuation of the Upper Miocene mammal world, for the carnivores, the perissodactyls—*Brachypotherium*, *Aceratherium*, *Tapirus*, *Chalicotherium*—the proboscideans—*Mastodon*, *Tetrabelodon*, and *Dinotherium*—are only little altered descendants of the Upper Miocene species. The same is true of the artiodactyls—pigs, deer, *Dorcatherium*, and the few antelopes; while even the apes, *Dryopithecus* and *Anthropodus*, may have been derived from *Pliopithecus*. The rodent fauna is extremely poor, because almost all the deposits of this period were formed either by great floods or by gravel-bearing rivers, and most small bones were destroyed: it consists chiefly of *Castor*, *Lepus* and *Dipoides*. The two latter genera came from the east, through Asia from North America, evidently at the same time as some *Felidae* and *Hipparion*. *Hyaena* is also an immigrant from the east. These few new faunal elements of western Europe are in sharp contrast to the multitude of new types which we meet with in South-eastern Europe and Western Asia. The Lower Pliocene fauna of Pikermi comprises a rhinoceros, *Atelodus pachygnathus*, different from the European forms; while on Samos and in Maragha there are further aceratheres resembling Chinese and Indian types. Quite unexpectedly there also appears here a large hyracoid, *Pliohyrax*. Specially characteristic also are the giraffes, *Camelopardalis*, *Helladotherium*, *Samotherium*, *Palaeotragus*, etc., which are absent entirely from the west. Further, there are *Palaeoryx*, *Protoryx*, *Protragelaphus*, and other antelopes; while in central and western Europe such are restricted to *Palaeoreas*, *Tragocerus* and *Gazella*. The hyaenas, as well as *Ictitherium* and *Mesopithecus*, are also decidedly eastern types. The fauna of Samos and Maragha leads us naturally to refer to the fauna of the Siwalik Hills, India, and of China. In the Siwalik, the greater part of the fossil mammalian remains belong indeed to the Lower Pliocene; but there is also an older fauna of European origin at least characterised by *Anthracotherium*, *Merycopotamus*, and a primitive species of *Hemimastodon*. *Dinotherium* and *Listriodon* perhaps also belong to this older fauna. The Pliocene fauna is distinguished by the occurrence of several primates—*Palaeopithecus*, *Sivapithecus*, *Simia*, *Macacus* and *Cynocephalus*. The beasts of prey are represented by *Canis*, *Amphicyon*, *Hyaenarctos*, *Ursus*, *Mellivora*, *Enhydriodon*, *Viverra*, *Machaerodus*, and comparatively numerous species of *Hyaena* and *Felis*. The genus *Mastodon* is likewise rather rich in species, and among the rhinoceroses there occur with European types some new forms which are of importance in the ancestry of existing species and also of *Rhinoceros antiquitatis* (or *tichorhinus*). With *Hipparion* there also appear here, as in China, species of *Equus*. The numerous *Suidae* have already a very modern aspect. With many deer we find giraffes, and the strange *Sivatheriinae* and numerous antelopes, which in part, as *Strepsiceros*, *Hippotragus* and *Alcelaphus*, live at present in Africa, like the genus *Hippopotamus*, which appears for the first time in the Siwalik fauna. No less important is the occurrence of *Camelus*, *Capra*, *Bubalus* and other *Bovidae*, although these perhaps belong to the younger *Stegodon*-fauna, which was so widely spread throughout Southern Asia. The mammalian remains in the red clays and

sandstones of China belong mainly to the genera just enumerated, which we regard as constituting the Siwalik fauna, or at least to very closely allied genera; some species are even identical with the Indian, although here there are also a few forms, such as *Anchitherium* and *Cervavus*, which evidently represent only descendants of the European Miocene types. At the end of the Miocene, North American faunal elements evidently invaded China, some of which, such as the *Leporidae*, *Dipoides*, *Hipparion*, *Canis* and *Vulpes*, perhaps also *Hyaena*, even reached Europe, while some at first spread only over Asia, such as *Camelus*, the aegodont antelopes, and perhaps also the *Sivatheriinae*, the descendants of *Protoceras*. As a return gift North America received the *Aphelops*-like rhinoceroses, *Palaeomeryx*-like deer, and especially the mastodonts, the carnivore *Dinocyon*, and perhaps also *Ursus*.

The fauna of Monte Bamboli and Casteani in Tuscany holds a peculiar position, for it contains the first European cynopithecine, *Oreopithecus*. Of the carnivores occurring here, *Hyaenarctos* is more primitive than that of Pikermi, the *Mustela* is very similar to a marten from Pikermi, and *Enhydriodon* to a species from the Siwalik, the antelopes can best be compared with those of Pikermi, and the pig is found also at Eppelsheim: this fauna must therefore be at the earliest of Lower Pliocene age. On the other hand, the fauna of Casino, notwithstanding its poverty, is connected rather with that of Rousillon and Montpellier, although the presence of *Hippopotamus* in it gives it a somewhat younger aspect. Contrasted with the Lower Pliocene mammal world, that of the **Middle Pliocene** appears somewhat poor. A considerable number of important species, such as *Machairodus crenatidens*, *Hyaena arvernensis*, *Ursus arvernensis*, *Mastodon arvernensis*, *Tapirus arvernensis*, and *Gazella borbonica*, as well as *Lagomys corsicanus*, are common to it and the Upper Pliocene; but it exhibits an older character by the presence of *Hipparion*, *Mastodon borsoni*, and perhaps also of *Rhinoceros leptorhinus* and a *Viverra*, while the numerous deer are still somewhat more primitive. Among the antelopes *Palaeoryx boodon* in some ways leads up to the cattle. While the rodents and the felines, in spite of their considerable variety, may not be of special interest, the occurrence of several *Cynopithecinae*, *Dolichopithecus Semnopithecus* and *Macacus* is all the more noteworthy. About the same time as this land fauna, there lived numerous marine mammals, especially toothed whales and some seals and sirenians—*Felsinotherium*, of which the remains appear in great abundance near Antwerp and Montpellier, in Piedmont and near Siena.

The **Upper Pliocene** mammal fauna of the Auvergne was early the subject of detailed investigation, and the most important of the species occurring here were later discovered in the Val d'Arno, Tuscany, while many of the characteristic forms were also found in England—Norwich Crag,—in Transylvania, and even near Giurgewo, in Roumania. While most of the deer and antelopes, pigs, tapirs, *Rhinoceros*, *Mastodon*, rodents and beasts of prey differ very little from their Middle Pliocene forerunners, and even belong in part to the same species, this fauna nevertheless bears a distinctly younger aspect through the first appearance of the genera *Elephas*, *Equus* and *Bos*.

In North America undoubted Pliocene is known only from Texas and Nebraska. The Blanco beds contain large canines—*Borophagus*, *Amphicyon*, a musteline—*Canimartes*, a feline—*Felis hillanus*, edentates—*Glyptotherium*, *Megalonyx* and *Mylodon*, several proboscideans—*Tetrabelodon* and *Mastodon*, horses—*Pliohippus*, *Protohippus* and *Neohipparion*, pigs—*Platygonus*, and camels—

Pliauchenia. Apart from the presence of the edentates, which arrived from South America, this fauna is characterised by the complete disappearance of the *Agriochoeridae* and *Rhinoceridae*. The deposits with *Elephas imperator* in Texas and Mexico may also perhaps be assigned to the Pliocene.

Pleistocene.

The **Pleistocene** begins both in North America and in Europe with a fauna which still contains species of a warm climate and even extinct genera. In North America the Sheridan formation of Nebraska and the Rock Creek beds of Texas are characterised by the first appearance of the genera *Equus*, *Antilocapra* and *Castoroides*, with *Elephas*, *Platygonus*, *Eschatius*, *Camelops*, *Felis*, *Canis*, *Lutra* and *Mylodon*; while the *Merycodus*-like *Capromeryx* has become extinct, and the rodents, except *Castoroides*, are represented only by existing genera. In Europe we find the oldest Pleistocene mammal fauna in the Cromer Forest Bed of England and Holland, at St. Prest (near Chartres), and at Mauer, near Heidelberg: the latter locality has become especially famous by the discovery there of a very primitive human jaw. The latest researches among the mammals found in these localities have shown, that between the Pliocene and Pleistocene there is no such sharp line of demarcation as might be supposed, for we still meet here with Pliocene species such as *Hippopotamus major*, *Equus stenonis*, *Rhinoceros etruscus*, *Elephas meridionalis*, *Ursus arvernensis*, *Canis neschersensis*, *Lynx issiodorensis* and *Hyaena arvernensis*. Some of these species, indeed, persist into the somewhat younger fauna of Mosbach, near Mainz, where they are associated with *Capreolus caprea*, *Cervus elaphus*, *Alces latifrons*, *Bison priscus*, *Sus scrofa* and *Castor fiber*, which then, with the exception of *Ursus deningeri* and *Alces latifrons*, reappear in all the younger Pleistocene deposits formed during a warm period, such as those of Taubach, Krapina, and the caves of Mentone. With them there also occasionally occur *Inuus*, *Hippopotamus*, and *Machairodus latidens*, as well as *Hyaena striata*. In Asia (China) during the older Pleistocene, *Hyaenarctos* and *Chalicotherium*, and a large tapir, still lived with *Rhinoceros sinensis* and *R. plicidens*, which to some extent represent the European *mercki*, also *Elephas namadicus*, hyaena, deer, and pig. To the older Pleistocene are also referable the fauna of the Narbada valley in India and the fauna of Trinil in Java, which has become so famous by the occurrence of *Pithecanthropus*, with *Macacus*, *Mececyon*, *Feliopsis*, *Stegodon*, *Rhinoceros*, *Hippopotamus*, *Sus*, *Cervulus*, *Axis*, *Duboisia* (related to *Boselaphus*), *Buffelus* and *Bibos*, all of which are represented only by extinct species sufficing to indicate the great age of this fauna.

In North America the true Middle Pleistocene appears to be characterised by the disappearance of *Camelus*, *Arctotherium*, and *Elephas columbi*, and their replacement by *Elephas primigenius*, *Mastodon*, *Odocoileus*, *Haploceras*, *Bison*, *Alces*, *Ovibos*, *Rangifer*, *Cervus* and *Ursus*; though at first there still occur machairodonts, *Megalonyx*, *Mylodon*, *Equus*, *Tapirus* and *Mylohyus*. A fauna of this period seems to be found in the famous Port Kennedy cave in Pennsylvania, perhaps also in the marls of western Kansas. *Megalonyx* and *Nothrotherium*, as well as *Equus* and *Elephas*, are also found in the Potter Creek cave in California, and at Silver Lake in Oregon. Most of the mammal remains, however, belong to still existing species of carnivores, rodents, deer and bison, among which indeed *Mastodon americanus* appears for the first time. Peculiar

Ovibos-like forms, which are now completely extinct—*Preptoceras* and *Euceratherium*—also occur here. The latest Pleistocene faunas of North America, for example, that from a fissure in Arkansas, consist only of *Equus*, a machairodont, and a musk-ox, *Symbos*, in association with species which still exist in North America.

The changes in the composition of the faunas, and the extinction or emigration of warmth-loving forms both in North America and in Europe, were determined specially by the extending glaciation. In North America the Conard fissure in Arkansas, already mentioned, seems to be the only known locality in which a larger number of the immigrant cold-loving species, or species adapted to cold conditions, have appeared; but in Europe the fauna of the true ice age plays a much more important part than the preglacial and interglacial mammal faunas of warmer habit. There are scarcely any caves in England, Belgium, France, Germany, Austria and Hungary where one would fail to find bones and other remains of cave bear, cave hyaena, reindeer, *Rhinoceros antiquitatis* and mammoth; while at times the cave lion, glutton, chamois, and wild goat, as well as saiga antelope and musk-ox, are associated with them. The species now enumerated have also often left their remains in the loess, more rarely in river deposits. Further, a not unimportant element of the latest European Pleistocene fauna are certain rodents—*Cuniculus*, *Lemmus*, *Ochotona*, *Dipus*, *Alactaga* and *Bobak*—which at present inhabit either the arctic tundra or the steppes of Russia and Western Asia. After the final retreat of the glaciers they withdrew indeed to their present habitats. Reindeer and musk-oxen also disappeared from the temperate parts of Europe, while the lion and hyaena were driven out of Europe by man. More difficult to understand, however, is the extinction of the mammoth, rhinoceros, and cave bear, for it can scarcely be assumed that man alone exterminated them as he killed off the giant deer, bison and aurochs.

African Region.

Until this century no fossil mammals were known from Africa except those from the Pleistocene of Algeria and a few fragments from the Tertiary of the same country. Nevertheless, Africa played an important part in zoogeographical speculations. It must have been especially the home of all the Pliocene mammals of Europe and Asia; there may also have been a great African-South American continent, and even the new forms now and then appearing in the European Eocene must have come from Africa. Now that we know remains of land mammals, both from the Eocene and Oligocene, and from the Miocene and Pliocene of Egypt, it is clear that these two later faunas comprise no other elements than the contemporaneous mammal faunas of Europe and Asia; and therefore that Africa, at least Northern Africa, already belonged faunistically to Eurasia. In the Eocene the land mammal fauna is confined to two genera, *Moeritherium* and *Barytherium*, which are both *Subungulata*; and the fauna of the Oligocene is distinguished by a peculiar mingling of indigenous forms, *Subungulata*—*Proboscidea*, *Palaeomastodon* and *Moeritherium*—*Hyracoidea*—the numerous *Saghatheriidae*—and *Arsinoitherium*, with immigrants from North America and Europe. From Europe originate *Ancodus*, *Apterodon*, *Pterodon*, and an indeterminable large creodont, the rodents *Phiomys* and *Metaphiomys*, and indeed also the bat, *Prorampyrus*. On the other hand,

descendants of old North American types are the *Primates—Parapithecus, Moeripithecus* and *Propliopithecus*, probably derived from *Anaptomorphidae*, the insectivore *Metolbodotes*, and probably also *Ptolemaia* and *Metasinopa*. The *Subungulata* are indeed the only truly African element, and even these may have been derived from *Condylarthra* or the most primitive placentals, and therefore be practically members of the old Arctogaean fauna. In no case are they more nearly related to the South American *Notoungulata*.

The existing and sub-fossil mammal fauna of the island of Madagascar exhibits a curious mingling of primitive and modern types. The latter are represented especially by the dwarf form of *Hippopotamus*, which has obviously come quite lately from the African continent; while *Cryptoprocta* is in fact only the descendant of a European Miocene carnivore. On the other hand, both the existing and the extinct lemurs, in part of gigantic size, can only be derived from the *Adapidae* of the European Eocene, while the *Centetidae* can only be considered as related to certain insectivores of the North American Eocene, with which they are geographically connected by the West African genus *Potamogale* and the *Solenodon*, which lives in Cuba.

South American Region.

For a long time the only fossil mammals known from the southern hemisphere were those from the pampas and the caves of Brazil in South America, and the extinct marsupials and monotremes from Australia. Our knowledge has only gradually been increased a little by discoveries in the Tertiary of Patagonia. The extensive collections of Ameghino in this region gave us the first real glimpse of the richness of the mammal fauna here entombed, which certainly exhibits a most unfamiliar character. Instead of the artiodactyl and perissodactyl ungulates and the proboscideans to which we are accustomed, here we meet with ungulates which have rather the outward appearance of rodents, such as the capybara, on account of their short skull, usually deep lower jaw, arched back, short and stout fore-limbs, low position of the head, and the short, generally three-toed, feet, often with blunt claws, only rarely with hoofs. Others are more like hares. Instead of bats, insectivores, and carnivores, we find marsupials, which remind us in part of the Australian predaceous marsupials, in part of the Mesozoic *Allotheria*. The *Edentata* also form an important element, appearing early, and indigenous to South America; while even the rodents, which appear later, belong to families which at the present day are almost exclusively confined to the same continent. However strange this mammal world may appear at first sight, yet certain resemblances to forms of the northern hemisphere are recognisable on closer consideration, for some of the hoofed animals, the *Litopterna*, which in dentition and limbs certainly look like caricatures of the perissodactyls, exhibit a certain relationship to the *Phenacodontidae*, and even the most peculiar *Typotheria, Toxodontia, Entelonychia* and *Astrapotherioidea* begin with forms which, in their molar teeth at any rate, are derivable from the *Periptychidae—Haploconus* and *Anisonchus*. Likewise, the *Gravigrada* are also traceable back to types of the oldest Eocene of North America, the *Ganodonta*; and the oldest representative of the armadillos was also perhaps an inhabitant of North America, the genus *Metachiromys*; while the marsupials, already mentioned, probably likewise originated in North America, partly from the

Allotheria and partly from the *Didelphys*-like types of the Upper Cretaceous Laramie beds. The rodents, which appear later, however, have another origin. Their ancestors lived in Europe and North Africa. They probably emigrated passively, having been carried from island to island by birds of prey; they therefore did not need a continuous bridge of land—a row of islands between West Africa and Brazil was sufficient.

The oldest deposits in South America from which mammals have been obtained in noteworthy numbers are the *Notostylops* beds of Casa Mayor, in the Gulf of St. George, Patagonia, which appear to be of about Upper Eocene age. Except the rodents, almost all the types of the South American fossil mammal world are already represented here, though at first by small or medium-sized forms always with brachyodont molar teeth, the *Typotheria* by the *Notopithecidae*, and perhaps also by the somewhat more distantly related *Archaeopithecidae* and *Acoelodidae*, the *Entelonychia* by the *Notostylopidae*, *Isotemnidae*, and *Homalodontotheriidae—Thomashuxleya*, the *Astrapothericoidea* by the *Trigonostylopidae* and *Albertogaudryidae*, and the *Litopterna* by the bunodont genus *Didolodus* and a number of other very imperfectly known forms. There are also already representatives of the very problematical *Pyrotheria*, of which *Carolozittelia* seems almost to suggest some relationship with *Pantolambda*. The *Polydolopidae*, which belong to the marsupials, remind us of the *Allotheria*; and the predaceous marsupials are represented by forms, such as *Procladosictis*, *Pharsophorus* and the *Didelphys*-like genus *Ideodidelphys*, with which may best be associated the peculiar bunodont *Caroloameghiniidae*. *Edentata* are by no means lacking, but most of the very problematical genera are already closely related to the existing *Dasypodidae*, and the single gravigrade genus, *Protobradys*, is only very incompletely known.

The next younger mammal fauna of Patagonia, that of the Oligocene *Astraponotus* beds, may be best described as the continuation of the *Notostylops* fauna, but it is certainly much poorer in genera and species, and is hitherto only very imperfectly known. As new types, there appear only the *Notohippidae*, of which the tooth-crowns are for the first time considerably hypsodont, the *Archaeohyracidae* with prismatic teeth, the *Astrapotheriidae—Astraponotus*—and among edentates the first *Glyptodontia*.

The succeeding fauna, that of the *Pyrotherium* beds south of Cape Blanco, shows much advance on the two preceding faunas, and has so many genera in common with the best known and richest fauna of Patagonia, the Santa Cruzian, that there cannot be any doubt about its Miocene age. The problematical *Pyrotheria*, which occur here for the last time, now reach the highest point of their development in the ponderous species of the genus *Pyrotherium*. The *Typotheria* and *Toxodontia* now all have prismatic teeth. The *Notohippidae* are also especially numerous here, and the *Nesodontidae* appear for the first time, even a large *Nesodon*, besides *Interatheriidae*, *Plagiarthrus*. Among *Entelonychia* the *Isotemnidae* are indeed extinct, but the *Leontiniidae* already attain great size of body—*Leontinia*, *Ancylocoelus*—likewise the *Astrapotheriidae*, and even the genus *Asmodeus* among the *Homalodontotheriidae*. The *Litopterna* are now specialised as *Proterotheriidae* and *Macraucheniidae*, but the latter are represented only by rather small brachyodont forms. Among the *Edentata* the *Dasypoda* are the direct successors of the forms in the *Notostylops* beds, while the *Glyptodontia* and *Gravigrada* are scarcely distinguishable from the later forms, and the same is the case with the *Dasyuridae*. On the other hand,

the *Polydolopidae* are extinct, and replaced to some extent by the first *Caenolestidae—Palaeothentes*, *Parabderites* and *Halmarhiphus*. The first immigration of rodents—*Cephalomys* and *Eosteiromys*—is especially noteworthy.

Intercalated between this fauna and that of Santa Cruz, both stratigraphically and morphologically, is the fauna of the *Colpodon* beds, which, according to Tournouer, are especially well developed at Lake Coli Huapi. Ameghino enumerates from it the very doubtful primates—*Homunculites* and *Pitheculites*—new types of rodents—*Acaremys*, *Spaniomys* and *Perimys*; among edentates, *Propalaeohoplophorus*; and among *Notohippidae*, which appear here for the last time, *Argyrohippus*, which is particularly interesting from the thickness of the enamel of its molar teeth. The *Entelonychia* already begin to be poorer in forms, so that the important genus *Colpodon* occurring here appears all the more abundant. *Typotheria*, *Litopterna* and *Astrapotheriidae*, as well as *Dasyuridae*, are unrepresented, which is especially remarkable; but the circumstance that the *Nesodontidae* appear to be now typically developed should not be overlooked. In age this fauna seems to correspond with that of the marine Patagonian formation.

The fauna of the Santa Cruz beds which now follows is the richest in species and the best studied of the whole of the South American Tertiary. Ameghino records several primates, among which only the genus *Homunculus* certainly belongs to this order. The *Nesodontidae—Nesodon* and *Adinotherium* —are remarkable for their great abundance; among the *Typotheria*, the genera *Protypotherium*, *Interatherium* and *Hegetotherium*, and the small *Pachyruchos* are not much behind these in the number of individuals. The *Entelonychia*, of which *Homalodontotherium* is the sole survivor, now become very rare, while the *Astrapotheriidae* are approaching extinction; but among the *Litopterna* the *Proterotheriidae* attain their maximum development, while the *Macraucheniidae* are distinguished from their forerunners by a considerable increase in bodily size. The rodents become unusually numerous, both the *Caviinae*, *Chinchillinae*, and of *Octodontidae*, the *Loncherinae* and *Capromyinae*; but of the *Hystricoidea*, only the *Acaremyinae* exhibit a noteworthy development. Among the edentates the *Megalonychinae* are distinguished by their special abundance, while the *Megatherinae* begin slowly to increase. The same may be said of the *Glyptodontia*, while the *Dasypoda* remain almost unchanged both in their organisation and in their abundance. Special mention should be made of the genus *Stegotherium*, which, from its long snout and reduced dentition, may lead to *Myrmecophaga*, as well as of the presence of an insectivore, *Necrolestes*, which reminds us of the African *Chrysochloridae*. The marsupials now reach the highest stage of their development in South America, not only the *Dasyuridae*, represented by the fine genera, *Borhyaena* and *Prothylacinus*, and the smaller *Cladosictis* and *Amphiproviverra*, but also the *Caenolestidae — Palaeothentes*, *Abderites*, and *Garzonia*, of which nevertheless only the last genus has left descendants. Lastly, the presence of a didelphyid, *Microbiotherium*, is also noteworthy.

The faunas between the Upper Miocene and the Pleistocene in South America are distinctly behind the earlier and later faunas, both in their variety and in their investigation. The Paraná stage is of marine origin, and therefore among mammals contains only *Cetacea*, *Pinnipedia*, and *Sirenia*, but of these a toothed whale, *Prosqualodon*, is of great interest. The land mammal fauna is characterised by the rarer occurrence of the *Litopterna* and *Typotheria*,

and the complete extinction of the *Dasyuridae*, *Palaeothentinae* and *Abderitinae*. Only one caenolestid—*Zygolestes*—and *Didelphys* are recorded from the Pliocene. *Toxodontinae*, *Macraucheniidae*, edentates and rodents form the main part of the fauna. Among the rodents also we often find forms which, like the representatives of the other groups just mentioned, are distinguished from their predecessors by a considerable increase in bodily size, such as *Megamys* of the subfamily *Chinchillinae*. The still existing genera, *Myopotamus*, *Lagostomus* and *Hydrochoerus*, also appear. The *Gravigrada* and *Glyptodontia* are in part already represented by genera of the Pampas formation, although the *Dasypoda* became poorer in the number of genera and species. True *Carnivora*—*Cyonasua*, *Arctotherium* and *Canis*—are also said to make their appearance.

An important and interesting fauna is that of the Tarija valley in Bolivia. It is at all events of essentially greater age than that of the Pampas formation, and contains in addition to the previous South American faunal elements—*Gravigrada*, *Glyptodontia*, *Dasypoda*, *Caviinae*, *Octodontinae* and *Capromyinae*—a number of forms which had hitherto been restricted to the northern hemisphere or even to North America. These newly appearing types are *Mastodon*, *Tapirus*, *Equidae*—*Hippidium*—*Cervicornia*, *Camelidae*, *Felidae*—*Smilodon*, *Felis*—*Ursidae*—*Arctotherium*—and dogs. *Mustelidae*—*Mephitis*—*Procyonidae*, *Leporidae* and *Hesperomyinae*, as well as *Dicotyles*, also reached South America at the end of the Tertiary, and then formed an important part of the South American mammal fauna in the Pleistocene. The original fauna became gradually poorer except in the long-established types of rodents, but the still surviving *Toxodontia*, *Gravigrada*, *Glyptodontia* and *Litopterna* of the family *Macraucheniidae* attained a very large size of body and often also extreme specialisation. In the older Pampas formation—Monte Hermoso—there are still *Typotheria*—*Pachyrucos* and *Typotherium*, as well as *Proterotheriidae*—*Epitherium*. The extinction of these small or only moderately sized forms may doubtless be ascribed to competition with the much better and serviceably organised mastodonts, artiodactyls, and perissodactyls, as well as to the activity of the immigrant beasts of prey. Gradually this competition and the ravages of the larger *Felidae* exterminated also the *Macraucheniidae*, *Toxodontidae* and the giant *Edentata*. If man, who arrived very late in South America, took part in the disappearance of these animals, he can only have exterminated the very last remnant of the old indigenous fauna. That he was really contemporary at least with one ground sloth, the *Glossotherium*, is certainly proved by the discoveries in the Eberhard cave on the gulf of Ultima Esperanza.

While the mammal faunas hitherto discovered in the South American Tertiary are confined to Patagonia, and the older Pleistocene faunas are hitherto known only from the Tarija valley in Bolivia and from Monte Hermoso, that of the later Pleistocene, the so-called fauna of the Pampas formation, has a much wider distribution. The principal localities in which it is found are still the northern parts of Argentina, but remains of species of the Pampas formation are also known from Chili and Brazil, while fragmentary remains of giant edentates are met with in the caves of Minas Geraes, Brazil, and also in the volcanic tuffs of Ecuador, although here in diminishing number compared with the horses and auchenias.

Australian Region.

We cannot close our account of the fossil mammal world of the southern hemisphere without a glance also at Australia, of which the mammal fauna is so strange compared with that of all the other continents. From the Tertiary here we know only the single genus *Wynyardia*, of which the systematic position cannot be satisfactorily determined on account of the lack of teeth. In the Pleistocene, however, especially in caves, we find remains of monotremes and a rather large number of marsupials, which in part attained gigantic body-size. They belong exclusively to forms which are more or less closely related to existing Australian genera, or are even in part referable to these genera. The Australian mammals are usually regarded as the descendants of Mesozoic forms, which by isolation here were able to develop undisturbed into great variety. Now, however, since the discovery of an important series of fossil *Polyprotodontia* and *Diprotodontia* in the Tertiary of Patagonia, we must ask the questions, whether the Australian types may not have been derived from these South American forms, and when they arrived in Australia. These questions are certainly not easily answered. The derivation of the Australian *Dasyuridae* from those of Patagonia presents no difficulties, but it seems scarcely permissible to trace back the *Hypsiprymnidae*, *Macropodidae* and *Phalangeridae*, as well as *Phascolomys* and *Diprotodon*, to the *Caenolestidae*—only *Thylacoleo* may perhaps come from *Abderites*; for in the *Caenolestidae* the molars are very unequal in size, while in the Australian *Diprotodontia* they are equal, and, moreover, in the first the front molar is not merely the largest, but also usually strongly differentiated. On the other hand, it is indeed very unlikely that there should have been no genetic connection between the Australian *Diprotodontia* and the South American *Caenolestidae*, while this is obviously the case with the Australian and South American *Dasyuridae*. The theory of a common origin has thus a certain justification. If the ancestral forms arose in South America and thence spread to Australia, this emigration can only have taken place across a very incomplete bridge of land, for otherwise the *Edentata*, *Litopterna* and *Notoungulata* would also have reached Australia. Nevertheless, it is not impossible that South America and Australia received the marsupials from a region so far unknown to us. In any case it would be a mistake to answer definitely at present the question as to the origin of the Australian mammals.

Conclusion.

As we have seen, the northern hemisphere is of much greater importance as a centre for the origin of the mammals than all other parts of the earth. Even South America, which was so prolific during the Tertiary, is by no means comparable, for it is not at all impossible that its mammal world originated from forms of the northern hemisphere, although connections between North and South America occurred only up to the middle of the Eocene and at the end of the Pliocene. Africa was a real centre of evolution only during the Eocene, and then merely for the *Archaeoceti* and the *Subungulata*, and even of these it is by no means certain that they were not derived from the mammals of the European Cetaceous. From the Oligocene onwards Africa was practically

a part of Europe. Lastly, so far as Australia is concerned, its mammal fauna seems to have immigrated comparatively recently, certainly not before the Tertiary. The theory of an Antarctic continent, which would be at the same time the home of certain mammalian types, such as the *Notoungulata* and *Subungulata*, receives no support from the geological history of the mammals.

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